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THE EVOLUTION OF THE HORSE. A RECORD AND ITS INTERPRETATION

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The American Museum of Natural History

INTRODUCTION

THE geological record of the Ancestry of the Horse is one of the classic examples of evolution. For this there are several reasons. First, the horse is a familiar animal; everyone knows what it is like, its habits, and is interested in learning how it got that way. Second, its fossil record is the most complete among the larger animals; and third, the outstanding changes in teeth and skeleton are obvious and easy to specify, and it is not difficult to understand their significance in animal mechanics and adaptation.

It has been a classic for fifty years or more, but the fossil evidence has vastly increased during that time, and especially during the last twenty or thirty years. Where Marsh and Cope and Leidy depended upon a few specimens, mostly fragmentary, we have today great series of complete skulls and skeletons; where their knowledge of the geologic succession was sketchy and generalized, ours is far more exact and certain. Yet there is very little to alter in what they had to say, although much to add; and it is the highest tribute to the insight and sound scientific method of these pioneers that their early work remains with but little change as the fc ndation of our present knowledge.

In this essay I shall attempt to give an outline first of the facts of record, the fossil evidence as it stands today, and second of the interpretation of that record, what it signifies and what it proves in the light of various aspects of modern research. So far as the facts are concerned, they are not cited from authority, but with very few exceptions are stated from first-hand knowledge and observation. Much of the detailed evidence on which these statements rest has been published by various authors, and the more important publications are listed at the end of the paper. Much of it is still unpublished material in the American Museum and elsewhere collected principally during the last few years. This unpublished material is responsible for various minor discrepancies between statements here made and those of previous writers. The interpretation of the evidence represents my

SKELETON OF EOHIPPUS IN AMERICAN MUSEUM OF NATURAL HISTORY, FOUND IN LOWER EOCENE OF BIGHORN BASIN, WYOMING, IN 1911

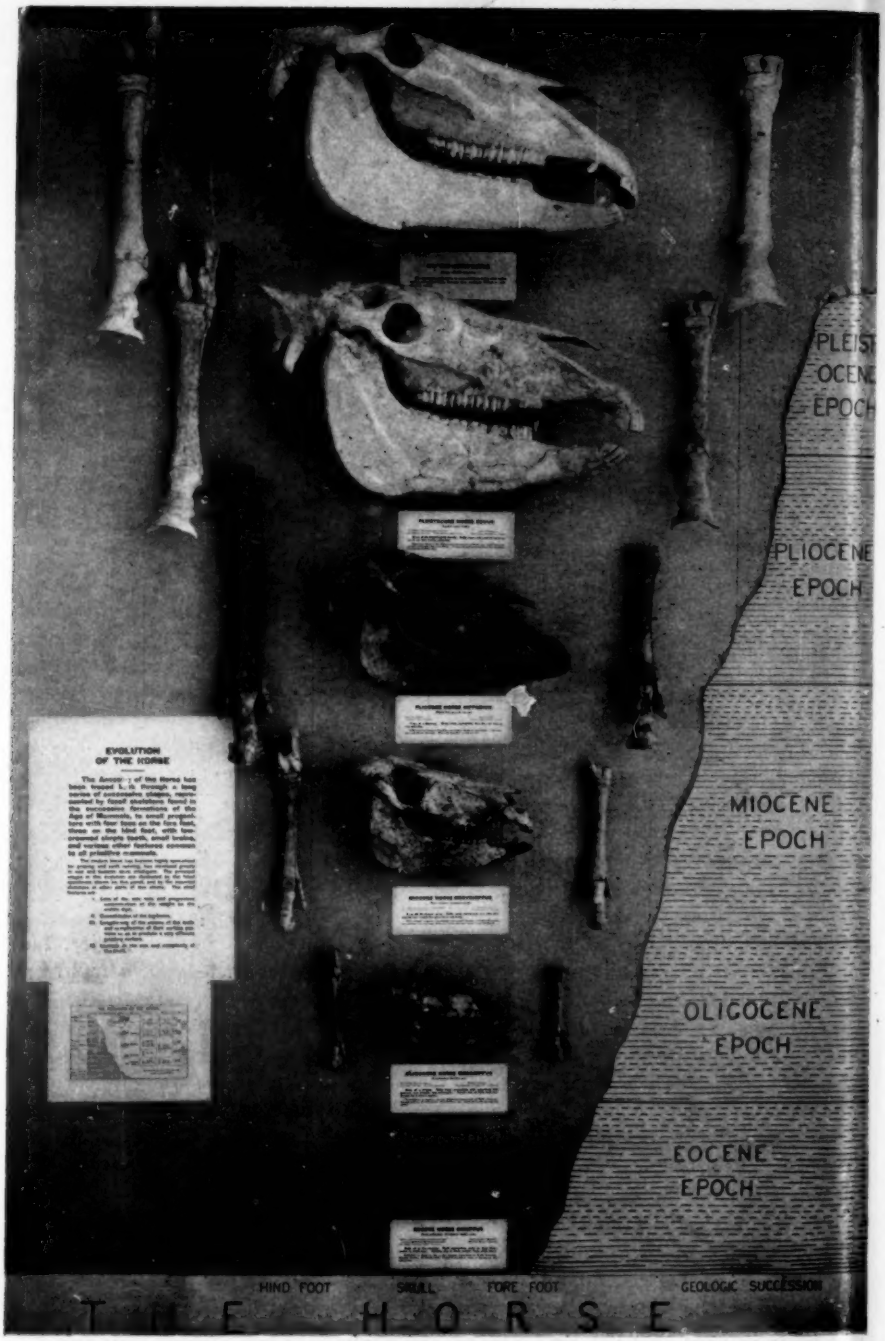

FIG. 1. DIAGRAM OF PRINCIPAL STAGES IN EVOLUTION OF TEETH AND FEET, WITH THE TERTIARY HORIZONS IN WHICH THEY ARE FOUND

[This diagram was recently republished without my authorization in a book called "The New Geology," with a caption stating that the succession here indicated does not exist, but that the specimens are arbitrarily arranged. The most charitable comment that one can make upon such a statement is that the author is utterly ignorant of the facts.]

own views, coincident in the main with those of most students of fossil vertebrates, but with various shades of divergence which more positive confrères may challenge as "errors" if they will. Within the space allotted it would be impossible

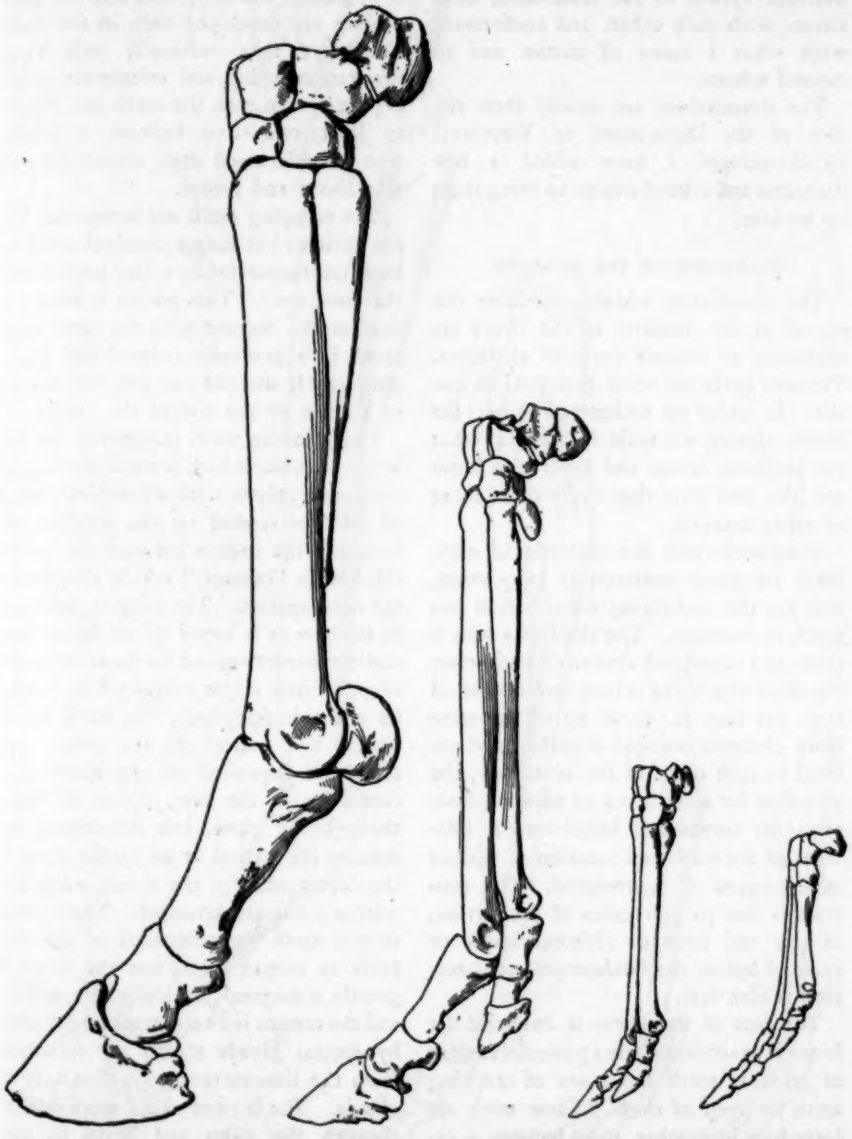

FIG. 2. STAGES IN THE EVOLUTION OF THE FORE FOOT: EOHIPPUS, MESOHIPPUS, MERYCHIPPUS AND EQUUS
External view, showing the progressive disappearance of the fifth and reduction of the fourth digit

to discuss such divergences of interpretation as may appear by comparison with the authorities cited. The views here outlined appear to me reasonable, consistent with each other, and conformant with what I know of nature and of natural science.

The illustrations are mostly from the files of the Department of Vertebrate Palaeontology. I have added a few diagrams and altered others to bring them up to date.

CHARACTERS OF THE SKELETON

The documents which constitute our record of the Ancestry of the Horse are skeletons or various parts of skeletons. The soft parts are never preserved as fossils. In order to understand what the fossils signify we must first know what the skeleton, bones and teeth of a horse are like, and how they differ from those of other animals.

Compared with the skeleton of man, there are many contrasts in proportion, and yet the underlying construction has much in common. The skull of a man is short and round and almost all brain-case; the skull of a horse is long and almost all face; yet they are made up of the same bony elements sutured together and related to each other in the same way, the processes for attachment of muscles, foramina for nerves and blood-vessels, relations of the teeth and location of various sense organs all correspond. The contrast is due to differences of proportion, of size and form of different bones or parts of bones; the fundamental construction is identical.

The face of the horse is extended far forward to accommodate a powerful battery of grinding teeth and a set of cropping teeth in front of them. These teeth are forty-four in number, three incisors, a canine, four premolars and three molars on each side of upper and of lower jaw; and all the permanent teeth except the molars and anterior lower premolars (p_1) are preceded by milk teeth. The p_1 however is very small and early lost, and the upper canines are developed only in the male. There are thus ordinarily only forty; fourteen cropping and twenty-six grinding teeth. In man the teeth are reduced to thirty-two—two incisors, a canine, two premolars and three molars on each side above and below.

The cropping teeth are somewhat like our incisors but longer crowned, with an inner crest separated by a deep pocket from the outer crest. This pocket is known as the "mark" because with the wear of the tooth it is gradually reduced and finally obliterated, and one can judge of the age of a horse by the size of the "mark."

The grinding teeth (excepting the first upper premolar which is small and simple) are square prisms with a complex pattern of infolded enamel on the wearing surface, and the valleys between the enamel filled with "cement," which also invests the outer surface. The prism is pushed up in the jaw as it wears off on the surface, and the harder enamel forms at all stages of wear little ridges supported by dentine on one side (originally the *inside* of the tooth) and cement on the other. The cement is deposited on the tooth as it comes up in the jaw, before it breaks through the gums, but the enamel and dentine are formed at an earlier stage in the development of the tooth, while it is within the dental chamber. These prism-shaped teeth are composed of the same parts as human teeth, but the crown is greatly elongated vertically (hypsodont) and the cement is a new structure deposited by special glands which are elaborated from the lime-secreting alkaline salivary glands. The crowns of the teeth push up through the gums and begin to wear before the roots are completed, but at 5–8 years the roots close, and thenceforth

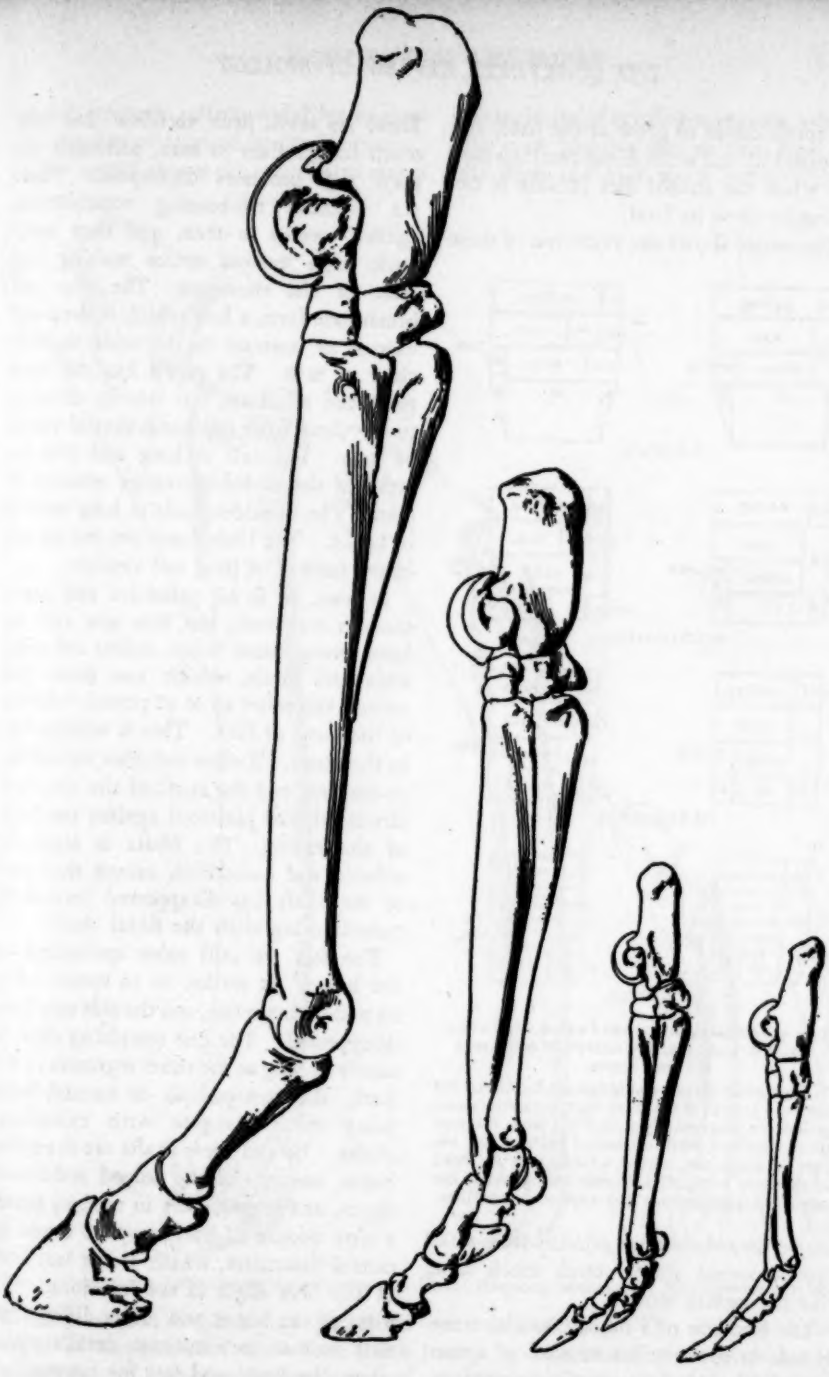

FIG. 3. STAGES IN THE EVOLUTION OF THE HIND FOOT: EOHIPPUS, MESOHIPPUS, MERYCHIPPUS AND EQUUS

External view, showing the disappearance of the vestigial fifth digit and reduction of the fourth digit to a splint.

the tooth ceases to grow at the base, and is pushed up and worn down until it is used up, when the animal dies because it can no longer chew its food.

The record shows the evolution of these long-crowned complex grinders from small short-crowned simple teeth much more like the human molar.

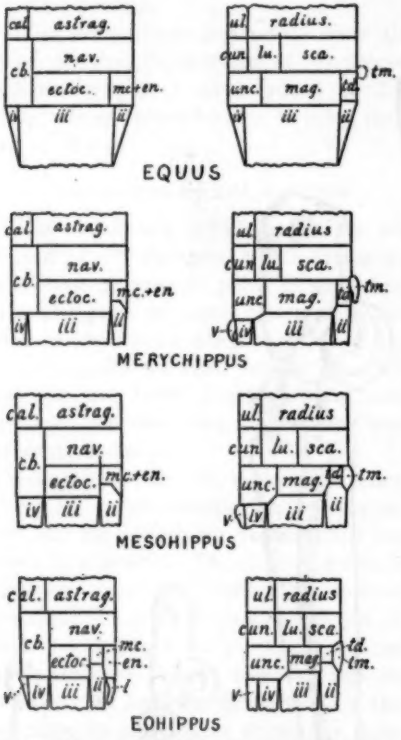

FIG. 4. DISPLACEMENT OF THE CARPAL AND TARSAL BONES IN EOHIPPUS, MESOHIPPUS, MERYCHIPPUS AND EQUUS

The median carpals and tarsals are broadened out with the growth of the third digit, the lateral metapodials are progressively pushed out from the support of the foot, while the lateral podial bones, except the trapezium, acquire a footing on the head of the third metapodial, thereby strengthening the carpal and tarsal joints at some expense in flexibility.

The skeleton of a horse likewise corresponds in construction to that of a man, again with wide differences in proportions. There are seven neck vertebræ, but very much longer than in man, although the parts and processes correspond. There are nineteen rib-bearing vertebræ as against twelve in man, and they carry quite high median spines making the crest of the shoulders. The ribs and breastbone form a box which is deep and narrow in contrast to the wide shallow chest of man. The pelvis has the same parts and relations, but wholly different proportions from the basin-shaped pelvis of man. The tail is long and free instead of the curled-in vestige retained in man. The shoulder-blade is long instead of broad. The limb bones are strong and heavy instead of long and slender.

In man, as in all primitive and many modern mammals, the fore arm and leg have two separate bones, radius and ulna, tibia and fibula, which can move one around the other so as to permit rotation of the hand or foot. This is wholly lost in the horse. Radius and ulna are solidly co-ossified, and the shaft of the ulna is a slender thread plastered against the back of the radius. The fibula is similarly reduced and co-ossified, except that part of the shaft has disappeared instead of consolidating with the tibial shaft.

The feet are still more specialized in the horse. It walks, so to speak, upon its middle fingernail, and the side toes have disappeared. The one remaining digit is nearly as long as the other segments of the limb, the metapodials or cannon-bones being much elongate with cylindrical shafts. Behind these shafts are the splint bones, vestiges of the second and fourth digits, and occasionally in modern horses a tiny nodule of bone may be found by careful dissection, which is the last trace of the fifth digit of the fore foot. The form of the bones and joints differs from that in man in numerous details which adapt the limbs and feet for locomotion,

giving strength and powerful leverage at the expense of most of its flexibility.

The record shows the progressive stages in the evolution of this highly specialized organ of locomotion from a foot much nearer that of primitive mammals and of the majority of existing mammals, which, like man, had five toes on each foot, and the limb and foot much better adapted to various uses. The earliest known stage in the ancestry of the horse has four complete separate digits of nearly equal

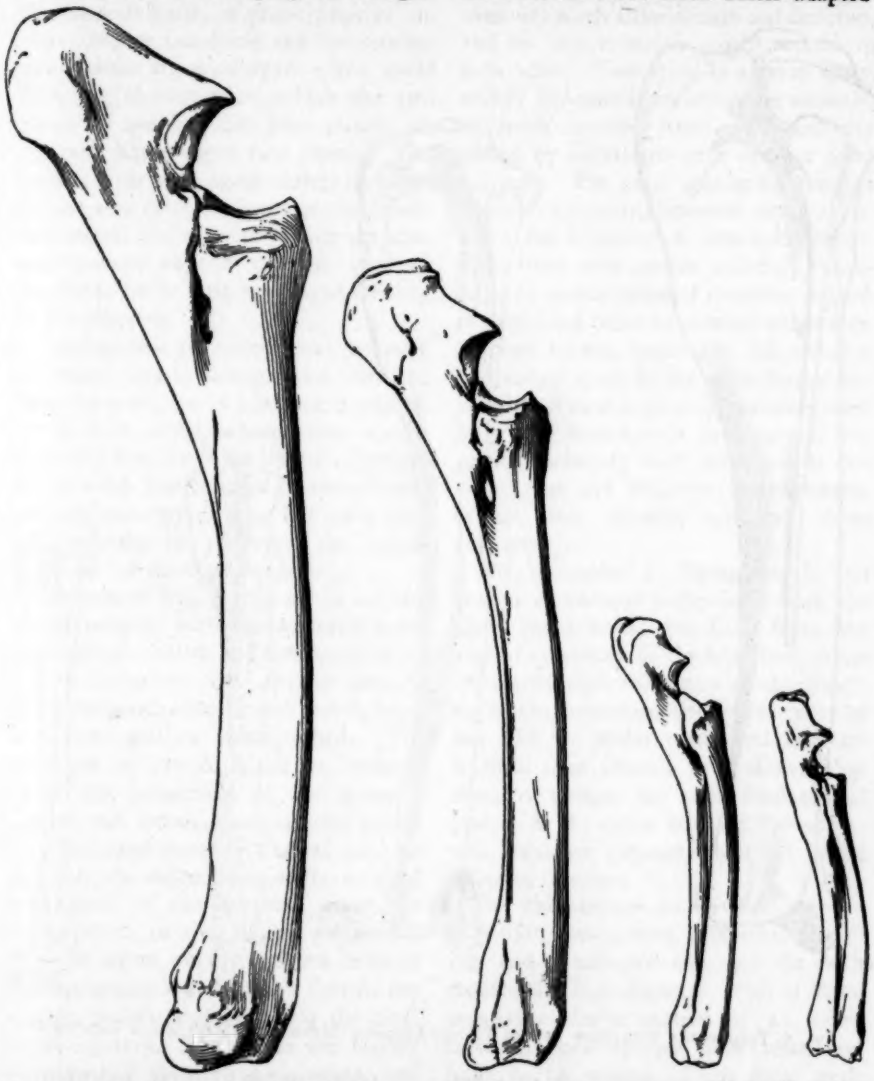

FIG. 5. PROGRESSIVE CONSOLIDATION OF RADIUS AND ULNA: EOHIPPUS, MESOHIPPUS, MERYCHIPPUS AND EQUUS

size on the fore foot, and three on the hind foot, with vestiges of the two missing ones. Future discovery may enable us to trace the ancestry back to a five-toed form.

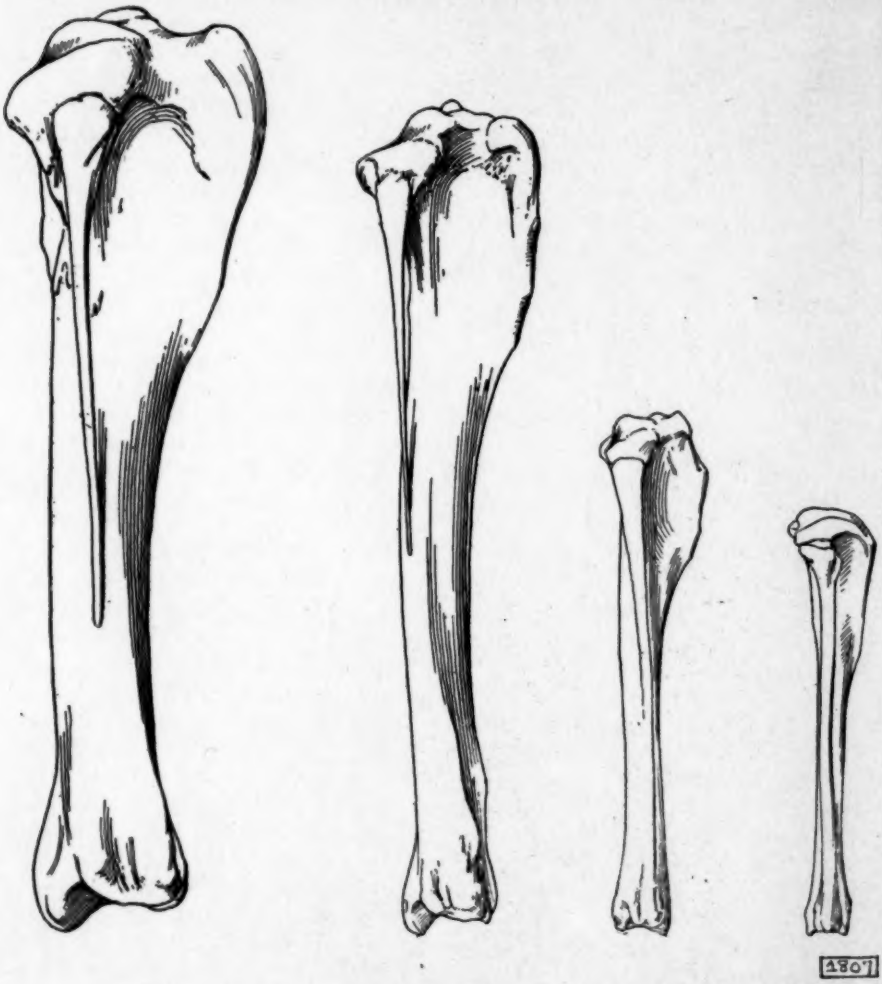

FIG. 6. PROGRESSIVE REDUCTION OF THE FIBULA: EOHIPPUS, MESOHIPPUS, MERYCHIPPUS AND EQUUS

Excellent accounts of the osteology of the horse, the development of the teeth, and its general anatomy may be found in various textbooks, especially Chubb (1921), Lydekker (1912), and Sisson (1910).

LIVING SPECIES OF HORSES AND THEIR RELATIVES

The breeds of the domestic horse vary widely in size and considerably in general

proportions, as well as in color and various superficial characters. The extremes of size in the Shetland pony and the Percheron draft-horse, of proportions in the slim compact race-horse and the massive plow-horse, are wide apart. Yet, aside from the characters on which the emphasis of breeding has been placed, all domestic horses agree very closely. The pattern of the teeth agrees closely throughout; so also there are innumerable details throughout the skeleton which are constant or very slightly varying. And all interbreed freely with no loss of fertility in the offspring.

The domestic ass has no great diversity of breeds, and is distinguished from the horse by a number of constant characters in the teeth, skull and skeleton, as well as by the sterility of the hybrid offspring. In the tooth pattern there are some details that are not very obvious but quite constant—notably the absence of the "caballine fold" of the upper molars.

The various wild species are in varying degree infertile with the domestic horse and with each other, and distinguished by surface characters often obvious enough, but all are much alike in teeth and skeleton and not easily distinguished. The wild ass of North Africa is believed to be the progenitor of the domestic species, and among the true wild horses and feral races found in Central Asia are probably the descendants of the original wild stock of the domestic horse. In Africa south of the Sahara are several kinds of zebras usually grouped in three distinct species still living; a fourth, the quagga, became extinct during the nineteenth century. The zebras are readily distinguished by the color pattern, and there are some differences among them in the form of the skull and other details, but in the teeth they are almost indistinguishable from each other or from the domestic horse.

All the species of the horse family are thus very much alike in teeth and skeleton, and by this criterion nearly related to each other. They stand in a group apart, widely different from any other animals, so much so that they were formerly placed by naturalists in a distinct order Solipeda. The great anatomist, Richard Owen, recognized however that underneath the diversity of form and proportions there were certain underlying identities in construction of skeleton, pattern of teeth, and other anatomical characters, between horses, tapirs and rhinoceroses, and united them in the order Perissodactyla or odd-toed ungulates, separating them from the Artiodactyla or even-toed ungulates including most other hoofed animals (pigs and peccaries, hippopotami, camels, deer, giraffes, antelopes, sheep and cattle).

The astragalus in Perissodactyla has always an oblique pulley-joint with the tibia, and a nearly flat distal facet; the axis of symmetry in the hind foot passes always through the center of the middle digit; the premolars always are more or less like the molar teeth, and later researches than Owen's have shown that there is always the same fundamental pattern in the molar teeth of Perissodactyla although variously modified in the different families.

The rhinoceroses have three toes on each foot, short, stout, somewhat spreading, and of subequal size, and the teeth moderately high-crowned with a comparatively simple pattern of an outer crest and two oblique cross crests, and little or no cement. Their front teeth have either been wholly lost or a single pair of stout lower tusks remains, sometimes also a pair of upper tusks. All

modern rhinoceroses have horns, one, or two arranged tandem.

The tapirs have four toes on the front foot, and three on the hind foot, their cheek teeth are short-crowned, with a simple pattern of cross crests, united by an external loop in the upper teeth; the front teeth are of cropping type, somewhat as in the horse, but lacking the inner crest and "mark." The muzzle is developed into a prehensile proboscis or short trunk, and the conformation of the skull considerably modified for attachment of the necessary muscles.

These three types of hoofed animals are very diverse in their external appearance, habits of life, and environment. The horses, living wholly in the open plains and feeding upon short dry grasses, swift footed, unarmed, escaping their enemies by flight, represent one perfected special adaptation. The rhinoceroses, living mainly in the bush and open forests, feeding upon the coarser grasses, leaves and twigs, powerful and heavily armored for offense and defense, represent a second specialized type. A third is seen in the tapirs, inhabitants of the dense forests and swampy jungle, browsing upon its lush vegetation, excellent at wading and swimming, hiding from their enemies in thicket or stream.

The fossil record of the Perissodactyla is exceptionally complete, and shows that horse, rhinoceros and tapir are three diversely specialized survivors of a large group of animals which were formerly much more abundant and were the principal hoofed animals of the older Tertiary. They included several other specialized groups now extinct, various intermediate types, and the record of all or most of these can be traced back through the Tertiary period, gradually converging into a common primitive stock. From this primitive stock, which appears in the known record near the beginning of the Tertiary period, can be traced through many successive intermediate stages the evolution of the horse, rhinoceros and tapir, the three surviving specializations, and also the ancestry of the Titanotheres, Chalicotheres, and other specialized types which have become extinct.

This record is derived from the succession of geological formations in the United States and in Europe, and the primitive Perissodactyla appear suddenly in both regions at the beginning of the true Eocene. Presumably they were invaders from some other region, not yet adequately explored by geologists, or in which the geological record has not been preserved. If the former, we may expect to discover the earlier stages of ancestry and to trace back the ancestry of these primitive Perissodactyla to a five-toed stage probably representing the common ancestry of these and other placental mammals. If the latter, the solution of the origin of the higher mammals will remain as it is now, dependent upon anatomical and other indirect evidence.

FOSSIL HORSES OF THE AGE OF MAN

Remains of horses have been found in the surface formations, of Pleistocene age, in all parts of the world. In the recent soils and sediments accumulated during the last few centuries, the bones are mostly those of domestic animals, and are not fossils in the customary sense of the word. They are little if at all altered by petrifaction, and belong to various breeds of the domesticated horse, *Equus caballus*. They are sometimes of interest to historians, archaeologists, or in researches into the origin of the various breeds of horse.

The Pleistocene horses, prehistoric and much more ancient, were contemporary with primitive man and with the great

Ice Age or Glacial Period. They cover a period from a few thousand years ago to the beginning of the Pleistocene variously estimated from a hundred thousand up to a million or more years old. They are found in all the great continents excepting Australia, and are referred to various species, some still existing, others extinct. In the New World all the fossil horses are extinct, and, in North America at least, appear to be limited to the older part of the Pleistocene; in South America they seem to have survived longer, and are believed by some authorities to have given origin to the herds of wild horses (mustangs) that ranged the Argentine plains as early as the sixteenth century A. D. The more generally accepted conclusion is that the existing wild horses in South America, as in North America, are all "feral," that is to say, escaped from domestication and not truly wild, and that they are the descendants of animals brought over by the Spaniards and other early colonists. They have the characters of the domestic species and interbreed freely with it.

In Africa, on the other hand, the Pleistocene horses have survived to the present day in the various species of zebra, and in the wild ass of Somaliland, the latter the progenitor of the domestic ass. The wild asses of central Asia, belonging to three or more closely allied species or sub-species, are slenderly proportioned, graceful and swift animals quite distinct from either the true horse or the domestic ass. In Central Asia there are also wild true horses, regarded as the probable progenitors of the domestic breeds. The modern horse is regarded by Ewart and others as derived from three distinct strains, one European, inhabiting the northern forests, a second, the steppes of Central Asia and eastern Europe, a third, the plains and deserts of North Africa and southwestern Asia. Whether these were all derived in turn from a wild species inhabiting Central Asia in the early Pleistocene, and whether they were separately domesticated by different primitive races, or brought with them from their early home in Asia and modified under domestication to suit the environment of forest, steppe and desert, are interesting questions not yet conclusively settled in the present writer's judgment.

All the modern horses, asses and zebras, and all the Pleistocene species of the Old World and North America, are very much alike in teeth and skeleton, so that it has been customary to include them all in the single genus *Equus*. There are considerable differences in size and proportions of the limbs, and more obvious diversity in color and markings of the skin, so that many modern systematists separate the zebras, asses and true horses into different genera. For the palæontologist it is more convenient to retain the old inclusive genus.

In South America, besides the various fossil species of *Equus*, two or more extinct genera of horses are found in the Pleistocene formations. The best known is *Hippidium*, distinguished by a peculiar construction of the nasal bones, certain quite marked differences in the pattern and form of the teeth, and considerably shorter legs and feet. A complete skeleton of this curious horse is in the Museo Nacional of Buenos Aires, casts of it in the American Museum and elsewhere. The purpose of the long slender nasal bones has been variously interpreted; some have thought the animal had a proboscis, others that it had large glands on the face in front of the eyes. More probably it means an extensive soft area behind the nostrils that might perhaps be inflated like the face of the Saiga antelope, and was related to some

kind of specialization of the nasal air-sinuses.

THE TERTIARY ANCESTORS OF THE HORSE

The record of the ancestry of the horse is obtained from the Tertiary formations of various western states. It may be advisable to say a word as to the succession of these formations. They cover wide areas in the western plains from Canada to Texas and in the broad intermontane basins further westward, the strata nearly always lying horizontal and exposed principally in the badlands and escarpments at the sides of the river valleys that traverse these plains and basin regions. Each formation contains its own definite and characteristic fossil mammalian fauna, and the sequence of these faunas is determined beyond cavil by their superposition or overlapping. The entire sequence of faunas has not been found superposed in any one locality; but by correlating the various incomplete series found in different localities the entire series is determined. The details of this correlation are fully set forth in Osborn's Cenozoic Correlation, U. S. G. S. Bull. 361, and in his forthcoming Monograph of the Titanotheriidæ, the latter including results of later researches.

In this succession of geological formations are found the remains of a succession of ancestral stages leading up to the modern horse; also corresponding stages leading to the rhinoceros, tapir, camel, deer, dog, cat, and many less familiar animals. Among these ancestral series, none is so extensive or so well documented as the Ancestry of the Horse, and little has been published in regard to the ancestral series of various other animals, which are, for various reasons, less satisfactory for elementary teaching, although equally conclusive to the special student.

The principal stages in the Equidæ evolution are as shown below:

Pleistocene	Glacial and Interglacial		10 *Equus*
Pliocene	Blanco		9 *Plesippus*
Lower Pliocene or Upper Miocene	Nebraska (Ogalalla)		8 *Pliohippus*
Middle Miocene	Deep River	Arikaree	7 *Merychippus*
Lower Miocene	Harrison-Rosebud	Arikaree	6 *Parahippus*
Upper Oligocene	White River: Protoceras beds		5 *Miohippus*
Middle and Lower Oligocene	White River: Oreodon beds, Titanotherium		4 *Mesohippus*
Upper Eocene	Uinta	Washakie	3 *Epihippus*
Middle Eocene	Bridger	Wind River	2 *Orohippus*
Lower Eocene	Wasatch	Wind River	1 *Eohippus*

Between these principal stages, defined by progressive steps in equine evolution which have generally been admitted by palæontologists as of generic value, might easily be intercalated a series of intermediates, not so well defined or sharply separated. The species of *Equus* from the older Pleistocene, are clearly more primitive in construction of skull and tooth pattern than those of the later Pleistocene and the existing species. The *Pliohippus* from the Lower Pliocene are distinctly nearer to the following stage, *Plesippus;* those from the transitional and uppermost Miocene strata are nearer to *Merychippus*, and in fact grade into that genus. In the *Merychippus* stage three sub-stages may be similarly distinguished, in *Parahippus* two, in *Miohippus* and *Mesohippus* two each (though not well separated on the present evidence). In *Orohippus* two

Parahippus
Lower Miocene

Miohippus
Upper Oligocene

Mesohippus bairdii
Middle Oligocene

Mesohippus montanensis
Lower Oligocene

Epihippus
Upper Eocene

Orohippus
Middle Eocene

Eohippus
Lower Eocene

FIG. 7

Equus caballus
Recent

Equus complicatus
Pleistocene

Equus stenonis
Lower Pleistocene

Pliohippus
Upper Miocene

Merychippus
Middle Miocene

FIG. 8

FIG. 7. UPPER MOLARS OF ANCESTORS OF THE HORSE, LOWER EOCENE TO LOWER MIOCENE. SHORT-CROWNED TEETH WITHOUT CEMENT. ALL NATURAL SIZE

FIG. 8. UPPER MOLARS OF ANCESTORS OF THE HORSE, MIDDLE MIOCENE TO RECENT. PROGRESSIVELY LONG-CROWNED TEETH WITH CEMENT INVESTMENT. ALL NATURAL SIZE

stages have been fairly well distinguished. All of the above stages are based on the geological and faunal succession; that is to say, they occur not contemporaneously but in successive geological formations or strata, and associated with correspondingly different faunas. It should be added that in each contemporary fauna there are several species, some more and some less progressive in certain respects or in the sum of their characters; these are not of course regarded as ancestral stages, but as showing the range of variation in the species living at any one time. From this preliminary summary we may turn to a more detailed examination of the facts of our record.

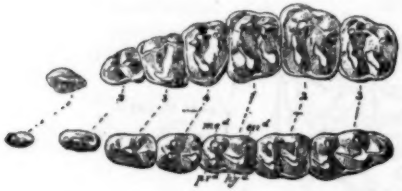

FIG. 9. EOHIPPUS RESARTUS. UPPER AND LOWER TEETH, NATURAL SIZE. LOWER EOCENE, BIGHORN BASIN, WYOMING. AFTER OSBORN

Stage 1. *Eohippus*. Lower Eocene. This is the classic Four-Toed Horse. The fore foot has four well developed, usable digits, but curiously enough no trace of the inner digit, or thumb. The hind foot has three well developed digits of subequal size, and small vestigial remains of the first and fifth digits, hardly more than little nodules of bone. The molars are quite short-crowned, with six main cusps partly converted into three crests, an outer crest, an anterior and a posterior inner cross crest, the three crests arranged in a characteristic pattern that suggests the Greek letter π. This pattern is the fundamental pattern of the primitive Perissodactyls. (It is still recognizable in the rhinoceroses, but has been altered out of all recognition in the modern tapirs and horses. Each phylum in the order has developed its own peculiar type of modification.)

The premolars are smaller than the molars, and of simpler pattern. The first two are simple-crested cutting teeth, the third and fourth have a large inner cusp, and the fourth has the main outer cusp twinned. In addition these two

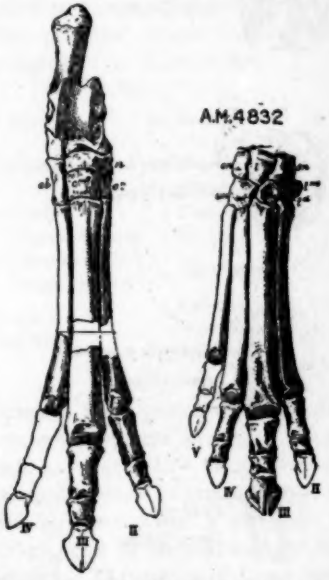

FIG. 10. EOHIPPUS VENTICOLUS. FORE AND HIND FEET, TWO-THIRDS NATURAL SIZE. WIND RIVER BASIN, WYOMING. FROM THE TYPE SKELETON, REDRAWN AFTER COPE

premolars have rudimentary crests and cusplets which in later stages develop into a molar pattern, so that these teeth in *Eohippus* are on the way to become molariform.

The limbs of *Eohippus* are also very primitive. In the fore limb, the radius and ulna are separate and complete, the shaft of the ulna moderately slender; in the hind limb the tibia and fibula are separate and complete, but the shaft of the fibula quite slender.

Eohippus thus has the normal limb and foot bones of mammals, except for the complete loss of the pollex or thumb, and the almost complete loss of the hallux or great toe and of the outermost digit in the hind foot. The tarsal bones, especially the astragalus, are characteristically Perissodactyl in their form and composition, and, while the ulna and fibula are separate and complete, their articulations are so changed that they permit of only very slight rotation of the foot. The modern tapir tarsus still retains the primitive construction of *Eohippus* little changed; in the rhinoceros it is broadened out, in the horse compacted and shortened.

Eohippus is commonly credited in text-books with a splint of the pollex, as shown in Marsh's drawing of 1876, was republished by Lull in 1907, and copied in various text-books. This is an error. Marsh had only a few fragments of the foot bones, from which he reconstructed the fore and hind feet; unfortunately he mis-identified some of the fragments, and supposed in consequence that there was a facet for a vestigial pollex, which he restored as a splint. The complete skeleton in the Cope Collection (described by Cope in 1885 as *Hyracotherium*), and a number of skeletons more or less complete found since that time, show that no trace of this vestigial pollex is present in any known species of *Eohippus*. Furthermore, in such animals as have a vestigial pollex, it never forms in the course of its reduction a slender, closely appressed splint such as is represented in Marsh's drawing. In all primitive mammals the pollex is sharply offset from the outer digits, affixed to the trapezium by a ball-and-socket joint, and moved by a special set of flexors and extensors, so as to be semi-opposable in the ordinary meaning of the term. This construction is something quite distinct from the merely divergent digits of many reptiles, and has an important bearing on the primary habitat of mammals.

Mr. J. W. Gidley, in a recent article, has confused the two, and has objected to the term semi-opposable, which however I still think entirely accurate as applied to the condition common to all Paleocene mammals, and one of numerous indications of a primary arboreal adaptation. The evidence to this effect will be published later in a memoir on the Paleocene mammalian faunas of New Mexico.

Thirteen species of *Eohippus* have been described, varying in size from that of a cat to a fox-terrier. Most of the material is fragmentary, jaws, parts of jaws and teeth, but three fairly complete skeletons are in the American Museum, one in the Amherst Museum. Many thousands of jaws and jaw-fragments have been obtained in the Lower Eocene of Wyoming and New Mexico, a few from Utah. The Lower Eocene of England, Belgium and France has also yielded a few specimens, the best a fairly good skull, described under the name of *Hyracotherium*, a name older than the more appropriate *Eohippus*, and hardly separable from it.

It is quite possible that certain species of *Eohippus*, when more intensively studied, will appear to be more directly in the line of ancestry of the horse, others of the tapir or rhinoceros or of some of the extinct phyla of Perissodactyls. A closely related genus, *Homogalax* ("*Systemodon*"), has been regarded as ancestral to the tapirs. This appears improbable in view of recent studies and of new evidence from the Mongolian Eocene; its relationships are rather with the Lophiodonts. In any event it is very close to *Eohippus*, and the feet are not distinguishable except by size, and absence of the vestigial first and fifth digits on the pes.

The American specimens of *Eohippus* come from various levels in the Lower Eocene strata, and one might expect to find progressive modification shown in the teeth from lower to upper levels, as is shown in a number of other contemporary mammalian phyla. Careful study, however, has failed to detect such evolutionary change, which would serve as a guide to the probable character of the next older stage in equine ancestry. *Eohippus* appears quite suddenly, in great numbers, at a particular level in the Wasatch formation, and was evidently an invading type, for nothing in the fauna of the underlying strata can be regarded as ancestral.

There is little doubt, however, that the ancestor of *Eohippus* is to be sought amongst the Condylarthra, primitive five-toed ungulates of which *Phenacodus*, a contemporary of *Eohippus*, is the best known form. Probably the earlier stages in the evolution of the horse will be found, if at all, in the Paleocene and late Cretaceous Condylarths of some intermediate northern region whence came the American *Eohippus* and European *Hyracotherium*. Central or northern Asia is the region indicated, but thus far no such animals have been found. The negative evidence from a few preliminary explorations has, however, no great weight, save to indicate that northern rather than Central Asia was the center of origin of the family.

2. *Orohippus*, the second stage in the evolution of the horse, is found in the Middle Eocene Bridger formation. One nearly complete skeleton is in the American Museum, a finely preserved skull and fore foot in the Yale Museum, but otherwise it is known only from jaws and fragments. These represent a number of species, some nearer to *Eohippus*, some more advanced in tooth characters, but with about the same range in size. The fore foot differs from *Eohippus* in slightly larger size of the central digit, the hind foot in the disappearance of the vestigial first and fifth digits, while in the teeth the molar crests are somewhat more pronounced and the third and fourth premolars have become more like the molars in pattern and size. The more primitive species of *Orohippus* are found only in the lower part of the Bridger formation, the more advanced species in the upper part, so that here we do have a progressive evolution in the species.

FIG. 11. MIOHIPPUS QUARTUS. UPPER TEETH, NATURAL SIZE. JOHN DAY BASIN, OREGON. AFTER OSBORN

3. *Epihippus*, the third stage in equine evolution, is imperfectly known. No complete skulls or skeletons have yet been found, but a large number of upper and lower jaws and various fragmentary skeletons with the fore and hind feet preserved in some of them. It carries on the line a step further in the somewhat higher-crowned and more sharply crested molars, the two posterior premolars are almost exactly like the molars in pattern, the central digit in both fore and hind foot is relatively larger, the fifth toe of the fore foot is smaller and more slender, although still a complete and usable toe. Its remains have been found in the Upper Eocene Uinta formation of Utah. The specimens are principally in the American

Museum, Yale, Princeton and Carnegie Museums.

4. *Mesohippus*, the fourth stage, is found in the Lower and Middle Oligocene formations of the western plains region from Saskatchewan to Colorado. Numerous skulls and many complete skeletons are known, and many thousands of jaws, feet and other fragments. There are various species, all much alike, and about the

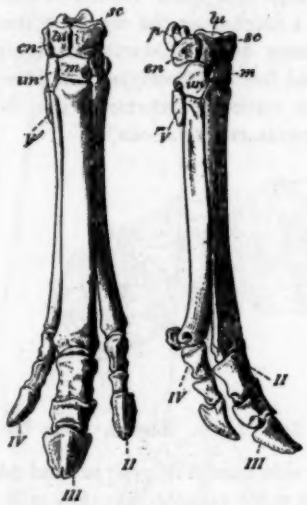

Fig. 12. Miohippus intermedius. Fore Foot, One-third Natural Size. Upper Oligocene, South Dakota. From the Type Skeleton, after Osborn and Wortman

size of a prairie wolf. It is a considerable step forward from *Epihippus*, and not quite in the line of trend indicated by the three Eocene stages. Three of the premolars are molariform, so completely so that they are not easily distinguished from the molars, and are slightly larger. The first premolar ($p\frac{1}{1}$) remains small and simple, tending rather to disappearance. The fore and hind feet are three-toed, the side toes much smaller than the central one, although they are complete and reach the ground in an ordinary step. Of the outer digit in the fore foot, complete in *Epihippus*, only a very short, small splint remains, hardly more than a nodule of bone. The shaft of the ulna, although still complete, is reduced to a thin, slender,

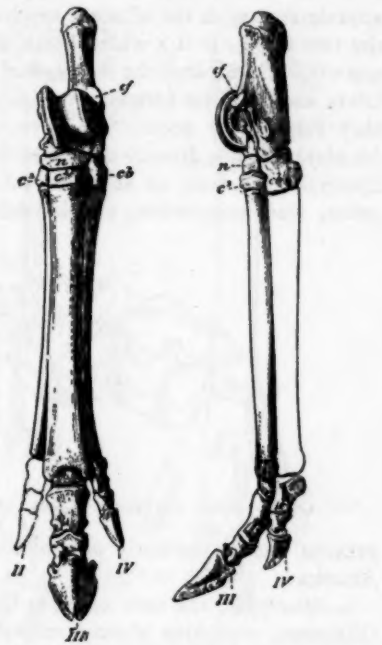

Fig. 13. Miohippus intermedius. Hind Foot, One-third Natural Size. Upper Oligocene, South Dakota. From the Type Skeleton, after Osborn and Wortman

The drawing is incorrect in failing to show the cuboid facet on metatarsal III, quite distinct on the original.

flattened rod, lying close to the back of the radius, although not co-ossified with it. The distal end of the bone is very apt to be co-ossified. The shaft of the fibula is still further reduced to a long delicate sliver of bone, the lower part lying against the tibia and partly co-ossified with it.

There is a considerable gap between

Epihippus and *Mesohippus*, which may be partly filled when we know more specimens and species of *Epihippus*, and have a better idea of its range and characters. The Lower Oligocene species of *Mesohippus* are also incompletely known, although they appear to be very close to the well known species of the Middle Oligocene. Even allowing for this imperfect acquaintance with the adjacent species of the two stages, it is a wider break than one would expect from the relations of the Uinta and Chadron formations in which they respectively occur. I believe that *Mesohippus* is not directly descended from *Epihippus*, but from an unknown related genus, more progressive, and inhabiting perhaps a more northerly part of North America.

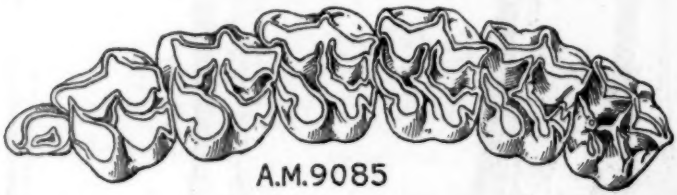

FIG. 14. PARAHIPPUS PAWNIENSIS. UPPER TEETH, NATURAL SIZE. LOWER MIOCENE, SOUTH DAKOTA

5. *Miohippus*, the next stage, is Upper Oligocene, and very closely related to *Mesohippus*, so that it is doubtful whether the two genera should be kept separate. Except that the species average larger in size, it can hardly be said to be more progressive. Marsh's classic diagram of 1892, which was republished by Lull in 1907, and copied in various text-books, represents the splint of the fifth digit as more reduced than in *Mesohippus*, but this does not seem to be the case. There is, however, one progressive step, not noticed by Marsh, and not invariable or constant, that generally distinguishes *Miohippus*. In the hind foot of *Mesohippus* the central metatarsal supports only the ecto-cuneiform bone of the tarsus; the cuboid and the inner cuneiform are wholly supported on the lateral digits as in all the earlier types. In *Miohippus* the cuboid has gained a footing on the central metatarsal, as in all the later horses. This is a mechanical advantage in the reduction of the lateral digits, giving the tarsus a more solid support on the central digit, that keeps it from "rocking." We shall see that at a later stage the inner cuneiform also acquires a footing on the central metatarsal or cannon bone. (Marsh's drawings of the hind feet of *Mesohippus* and *Miohippus* do not correctly represent the normal tarso-metatarsal relations).

The side toes in *Mesohippus* and *Miohippus* are much reduced, but they still reach the ground and help to support the limb. This is partly because of the unusual shortness of the phalanges, or toes proper. This proportion is rapidly and progressively changed in the next stage in the direct line, but is continued for some time in the *Hypohippus* side branch.

6. *Parahippus*, the sixth stage, is found principally in the Lower Miocene formations over a much wider area, from Montana to Texas, and many skulls and incomplete skeletons are known. The various species cover a very considerable range in size and advance in structure, some not easily distinguished from *Miohippus*, while others are hardly separable

from *Merychippus* of the Middle Miocene. The older species geologically are more primitive, and the later species more progressive in general, but there is no uniform progress among them, some being more advanced in size, some in structure of the teeth, some in structure of the feet. They suggest a group of related species of high individual variability with perhaps a good deal of hybridizing among different races. The result, however caused, is a rapid advance of the race during the Lower Miocene.

The tooth pattern changes by the progressive conversion of the two transverse crests into a pair of crescents at first oblique, tending to become antero-posterior in direction, while the inner pillars of the crests, especially the anterior one, become more or less separated. This change is continued and completed in the various species of *Merychippus*. At the same time the valleys between the crests begin to fill up with a new structure the *cement*, formed primarily as a deposit of "tartar" on the crown and during the period that

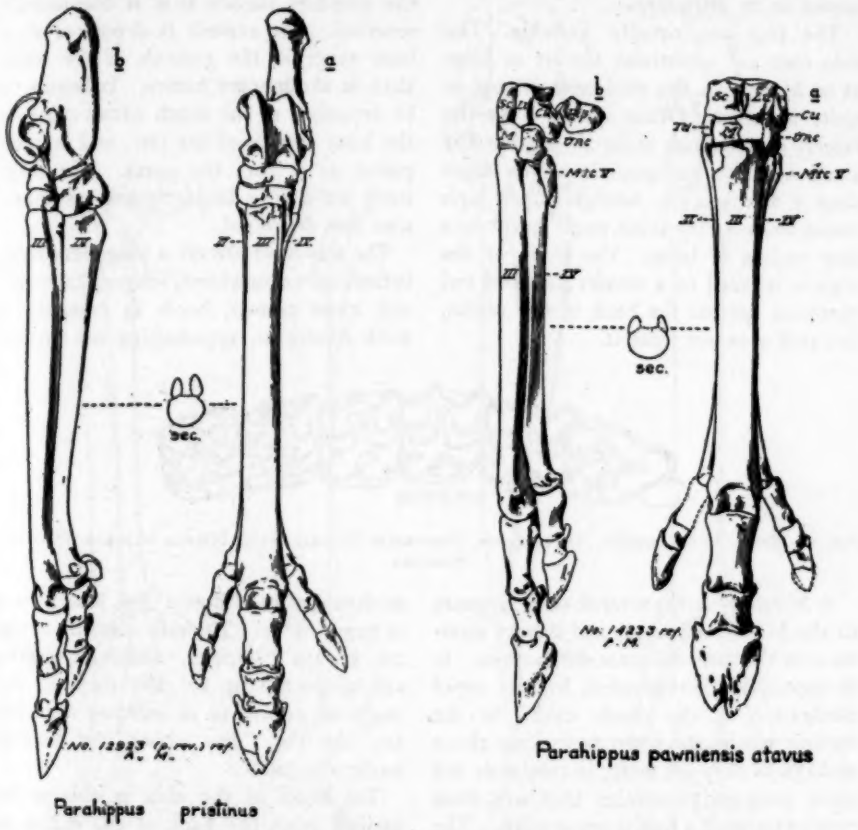

FIG. 15. FORE AND HIND FEET OF PARAHIPPUS, TWO-FIFTHS NATURAL SIZE. LOWER MIOCENE, SOUTH DAKOTA. AFTER OSBORN

the tooth is emerging from the jaw. The cement in *Parahippus* is usually a rather thin coating, sometimes more considerable; in some of the latest and most progressive species it completely fills the valleys and invests the outside of the crown as in *Merychippus*.

The feet are equally variable. The side toes are sometimes almost as large as in *Miohippus*, the phalanges almost or quite as short. Other species have the lateral digits much reduced, so that the shafts of their metapodials are no larger than a match. The vestigial fifth digit varies from a very short small splint to a tiny nodule of bone. The shaft of the ulna is reduced to a slender flattened rod plastered against the back of the radius, but still separate from it.

The permanent teeth are heavily coated with cement, which fills the valleys and invests the outside, so that in wear the enamel is everywhere supported on one side by cement, on the other by dentine, and as in modern horses makes a ridge on the grinding surface that is continually renewed. The cement is deposited at a later stage in the growth of the teeth than in the modern horses. It begins to be deposited as the tooth comes close to the bony surface of the jaw, and is completed as it cuts the gums. The milk teeth have very little cement on them, also late deposited.

The feet have always a long, relatively cylindrical cannon bone, longer phalanges, and more convex hoofs in comparison with *Miohippus*, approaching the smaller

FIG. 16. MERYCHIPPUS PANIENSIS. UPPER TEETH, TWO-THIRDS NATURAL SIZE. MIDDLE MIOCENE, WESTERN NEBRASKA

7. *Merychippus*, the seventh stage, appears in the Middle Miocene, and is very common in the later Miocene formations. It is especially distinguished by the rapid elongation of the cheek teeth. In the earliest species the upper molars are about as high as they are wide; in the latest and most progressive species they are from two to two and a half times as high. The milk teeth are short-crowned, as one would expect of milk teeth, but are disproportionately so, and their pattern is decidedly archaic, very like that of *Parahippus*. The permanent molars and premolars have the pattern converted into a pair of outer crescents, a pair of inner crescents and a pair of inner pillars, the anterior one more or less separated in different species.

modern species of horses (ass, kiang, etc.) in proportions. The side toes, however, are always complete, although slender and shortened up so that they do not reach the ground in an ordinary step, but are like the "dew claws" of various modern animals.

The shaft of the ulna is always coossified with the back of the radius in adult *Merychippus*, separate in the colts.

Twenty-five species of *Merychippus* have been described, many of them probably invalid or sub-species, but the genus is very wide-spread and abundant, and covers a considerable range of variation. It is found from Florida, Texas and California to Montana and Oregon.

In many species of *Merychippus* there is a marked hollow or fossa upon the side

of the face in front of the orbit. It is sometimes broad and shallow, sometimes deep and more or less restricted into a deep pocket, and frequently divided more or less clearly into two pockets, the lachrymal and malar fossae. One or both of these fossae are retained in many species of the later horses, but they have completely disappeared in *Equus*. Their significance has been disputed; some authorities have thought that they were analogous to the lachrymal fossae on the face of ruminants, lodging a scent-gland; others have seen analogies to the pockets that lodge the proboscis muscles of the tapir. It seems more probable however that they lodged an enlarged diverticulum or extension of the small blind sac that opens just within the nostrils of the modern horse; but the functions of such

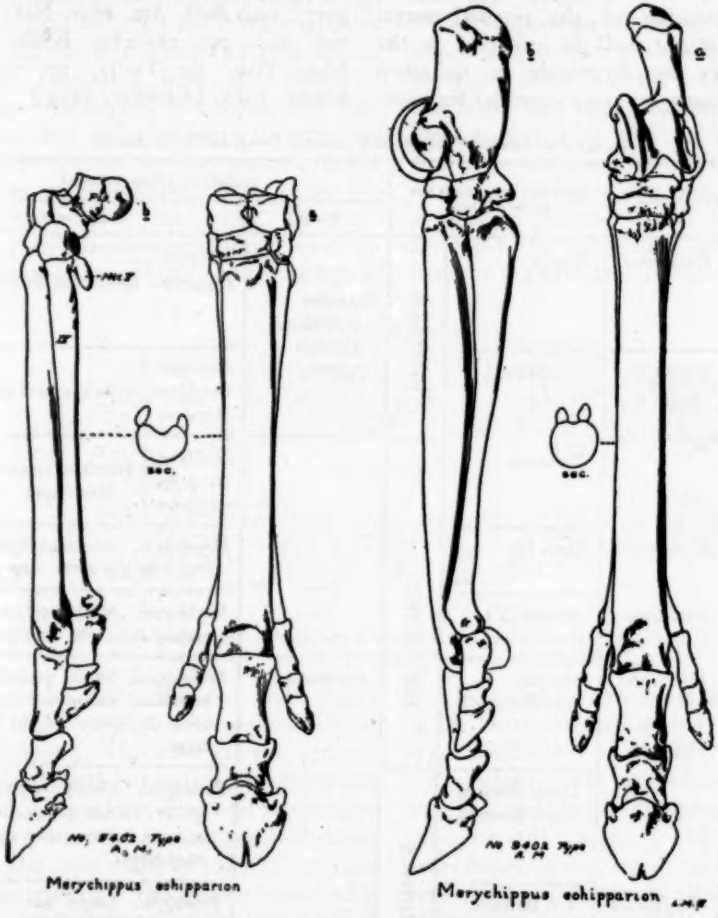

FIG. 17. MERYCHIPPUS EOHIPPARION. FORE AND HIND FEET, ONE-THIRD NATURAL SIZE. MIDDLE MIOCENE, COLORADO. AFTER OSBORN

an organ have not been made clear. The writer regards the appearance of these fossae as primarily conditioned by certain mechanical needs in bracing a progressively enlarging skull; and that the spaces later required for the elongated teeth and extension of the internal nareal bones, might well be occupied in the meantime by diverticula of unknown but perhaps not very essential function, which disappeared as the space was required for more important uses. The very variable occurrence of the fossae in the different species is difficult to reconcile with their serving any very essential functional purpose. (See Gregory, 1920 Bull. Am. Mus. Nat. Hist., vol. xlii, pp. 265–284; Boule, 1920, Mam. Foss. de Tarija, pp. 106–110; Studer, 1910, Lydekker, 1893.)

Geological distribution of later tertiary equida in Europe and North America

EPOCHS AND STAGES		AMERICAN FORMATIONS AND GENERIC ZONES		OCCURRENCE OF EQUID GENERA	
				Europe	North America
Pliocene	Plaisancian	Blanco	HIPPARION	*Hipparion.* Specialized aberrant species	*Plesippus* *Hipparion.* Specialized aberrant species
MIOCENE	Pontian	Republican	HIPPARION		*Pliohippus* *Protohippus* *Hipparion* } more advanced species
		Valentine	MERYCHIPPUS	*Anchitherium*	*Pliohippus* *Protohippus* *Hipparion* } Primitive species close to *Merychippus*
	Sarmatian	Santa Fé	MERYCHIPPUS		*Merychippus.* Advanced species passing into the three later genera.
	Tortonian	Pawnee Cr'k.	MERYCHIPPUS		*Merychippus.* Most larger species, forecasting the three later genera.
	Helvetian	Mascall L'r. Sheep Cr'k.	MERYCHIPPUS		*Merychippus.* Small, primitive, wide individual variation, which forecasts the species of the following stage
		Upper Harrison Upper Rosebud	PARAHIPPUS		*Parahippus.* Widely varying distinct species, mostly progressive in one or more features, some approaching *Merychippus*
	Burdigalian	L'r. Harrison	PARAHIPPUS		*Parahippus.* Larger and smaller species, rather primitive
		Lower Rosebud Monroe Cr'k.	PARAHIPPUS		*Parahippus.* Small primitive species. *Miohippus.* Mostly large and specialized species
	Aquitanian	John Day	MIOHIPPUS	No Equida	*Miohippus.* Larger and smaller species

The geologic occurrence of *Merychippus* is in the middle and upper Miocene "Merychippus Stage." The first appearance is in the Lower Sheep Creek Beds (Zone) and equivalents, with small primitive species; in the next following Pawnee Creek Beds are larger and more progressive species, and in the Santa Fé beds species hardly separable from the following genera *Protohippus*, *Pliohippus* and *Hipparion*, and mingled with others that must be referred to these genera. A few species of *Merychippus* linger in the Republican beds, then they disappear.

8. *Pliohippus*, the eighth stage, is a direct outcome of one of the species groups of *Merychippus* (*M. campestris* and allies), and is at first difficultly separable from *Merychippus*. The teeth become progressively longer, but retain the transverse width, simple lines of enamel surrounding the "lake borders," strong inward curvature and close union of inner pillars with inner crescents. The genus is more readily distinguished by its milk teeth, which are much higher-crowned (one and a half times to twice as high) as in *Merychippus*, a fourth to a third narrower transversely, and quite heavily cement-coated, as in modern horses.

The skull is large in proportion to the skeleton, different species varying from less than the size of the ass to equal to a small domestic horse. The fossæ, or pockets on the sides of the face in front of the orbits, are deep and extensive in all the older known species, shallow in some later species.

The proportions of the feet are more robust and heavier than in *Merychippus*, averaging about as in the modern Kiang; the larger and more progressive species have stouter limb and cannon bones. The inner cuneiform has shifted over to acquire a footing on the cannon bone, a progressive character earlier acquired by the *Hypohippus* side branch, but appearing here for the first time in the direct line.

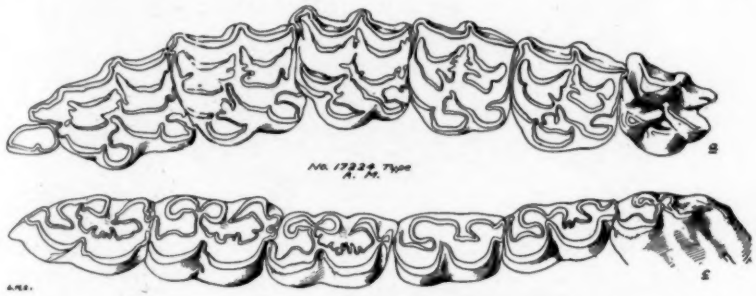

FIG. 18. PLIOHIPPUS LEIDYANUS. UPPER AND LOWER TEETH, TWO-THIRDS NATURAL SIZE. FROM THE SKELETON, UPPERMOST MIOCENE, NEBRASKA. AFTER OSBORN

The footing is not so broad and solid as in the Pleistocene and modern horses. It is not conditioned by the reduction of the lateral digits, for it occurs in *Hypohippus*, and in a species of *Pliohippus* in which these are still complete. Nor by robust proportions or size, since it occurs in the very small and extremely slender species of *Hipparion* from the middle Pliocene of Florida and Texas, also in all the Old World *Hipparions*, but not in most of the American species of this genus.

Pliohippus is said to be one-toed, and without question the lateral phalanges were greatly reduced or totally absent in some species. No adult specimens, how-

ever, show any of the lateral metapodials complete down to the expanded knob or plate which represents the distal end of the complete bone, and, in a juvenile skeleton described by Troxell as monodactyl, the form of the tip is certainly not that of a completely calcified end, so that it is doubtful whether bony phalanges would not have calcified before the animal became adult. On the other hand, in at least one species of *Pliohippus* from Texas, perfectly typical as respects its skull and teeth, the lateral digits have a complete set of phalanges, proportioned as in an average *Merychippus*. On the whole it seems probable that the toes in *Pliohippus* were in the same unstable condition as the teeth in *Parahippus;* some species had side toes and others did not, but there was a general reduction of the laterals and advance of the foot bones in all details in the direction of *Equus*.

9. *Plesippus*, the ninth stage, is known from the later Pliocene of Texas and California, but until 1924 so imperfectly (a few teeth only) that it could not be characterized and distinguished as a separate generic stage. In 1924 Mr. George Simpson and I found two skeletons at Mount Blanco, Texas, that between them give almost every detail of the anatomy. The animal compares in size and most proportions with the Arab horse, but the hoofs are much smaller, the back

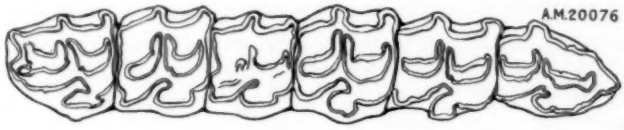

FIG. 19. PLESIPPUS SIMPLICIDENS. UPPER TEETH, ONE-HALF NATURAL SIZE. FROM A SKELETON, MIDDLE PLIOCENE, TEXAS

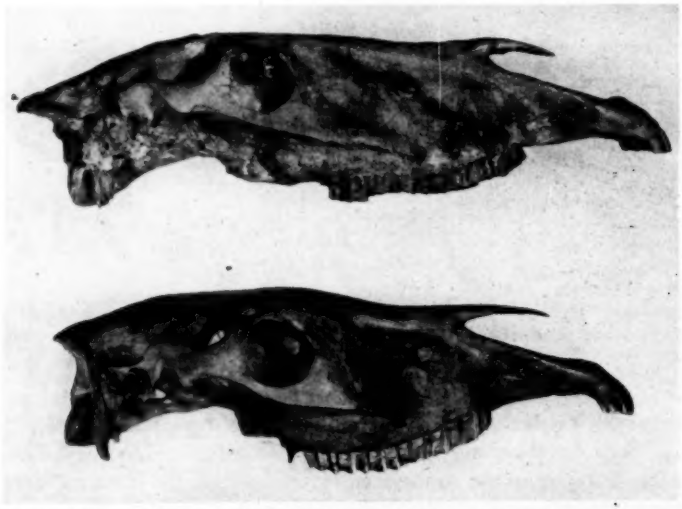

FIG. 20. PLESIPPUS SKULL FROM MIDDLE PLIOCENE OF TEXAS, COMPARED WITH MODERN EQUUS SKULL. ONE HALF NATURAL SIZE

shorter and the barrel less rounded and convex.

The teeth are like those of *Pliohippus* in pattern, but with longer crowns, much less curved (as in *Equus*); the pattern in various details makes some approach to *Equus*, but on the whole the tooth characters come nearer to *Pliohippus*.

The feet on the other hand are very much like those of *Equus* in proportions and general appearance. The lateral digits are reduced to splints, which end however in a thin flattened and expanded sliver instead of the little knob of *Equus*. They are slightly longer. The vestigial fifth metacarpal is retained on the outer side of the fore foot, and the trapezium on the inner side, as tiny nodules of bone, relatively smaller than in *Merychippus* and *Pliohippus*. In *Equus* these bones are occasionally calcified, but not normally present.

The fibula is reduced to a splint which in *Plesippus* is distinctly shorter than in

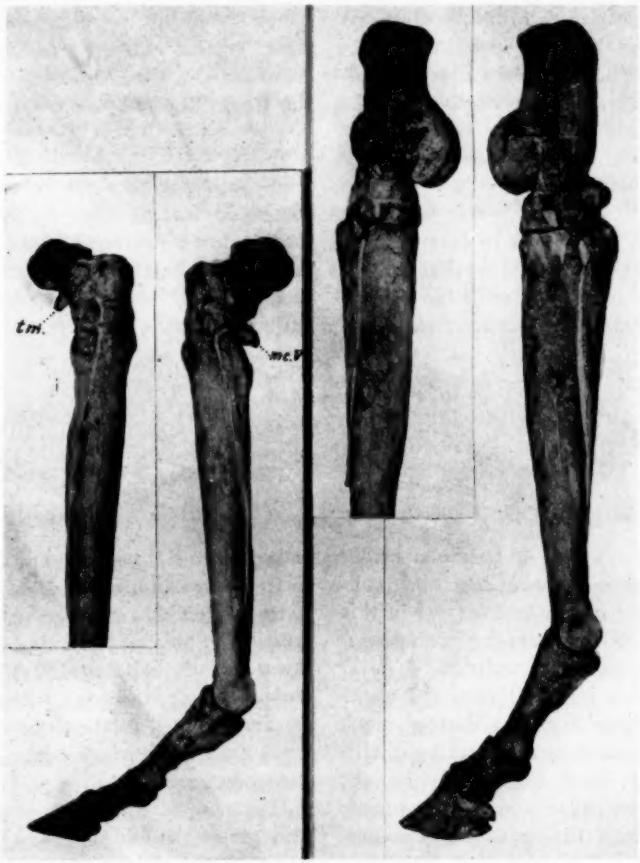

FIG. 21. PLESIPPUS FORE AND HIND FEET (PHOTO), FROM SKELETON. MIDDLE PLIOCENE, TEXAS. SHOWING VESTIGES OF FIFTH DIGIT AND TRAPEZIUM

any species of *Equus*. Probably this is a variable non-adaptive character in the later Equidæ; it is as far advanced in *Merychippus* as in *Equus*, further advanced in *Plesippus* and in some species at least of *Hipparion*.

The skull of *Plesippus* is remarkably *Equus*-like in size and proportions. It has acquired the long straight lines of the face, as opposed to the shorter proportions and more convex outlines of the head in the older Equines. It has almost completely lost the deep facial pockets of *Pliohippus;* only slight shallow hollows remain.

10. *Equus*. Pleistocene to Recent. The earliest certain recorded appearance of *Equus* proper is at the base of the Pleistocene in America and Europe. *Equus stenonis* of the Arno valley in Italy is a rather small species, primitive in the tooth construction, and nearer to *Plesippus* in this and other details than are the later species. Still it has the characteristics of *Equus* in the anterior inner pillar of the upper molars, flattened, with a narrow much constricted commissure connecting it with the anterior inner crescent, while the posterior inner pillar is reduced and tends to merge into the posterior crescent. The classic Val d'Arno and Asti fossil mammals have been generally called Upper Pliocene. According to the more recent correlation they are Lower Pleistocene. The older Pleistocene formations in North America contain remains of various species of the genus. Some are apparently as primitive as *Equus stenonis*, others as advanced in teeth as the modern horse. The few that are known from skulls and skeletons are distinct species, but not widely different from *E. caballus*.

Equus is a cosmopolitan genus, and has been found fossil in all parts of South America, in North America (except within the glaciated area), in practically all countries of Europe and Asia, in Africa from Algeria to Natal, failing to reach Australia and the islands that lie beyond the limits of the continental shelf.

DIVERGENT LINES OF EQUIDÆ

In the preceding pages the direct line of succession leading from *Eohippus* to the modern horse has been described. There are also a number of side branches, more or less closely related. The living zebras and asses, although different in color-

FIG. 22. EQUUS SP. UPPER TEETH, ONE-HALF NATURAL SIZE. LOWER PLEISTOCENE, NEBRASKA

pattern, size and proportions, are so close to the domestic horse in skeleton that it is very difficult to distinguish their fossil remains. Some of the extinct species of *Equus* are thought to be especially related in teeth to the zebra, others are more certainly related to the ass; but the three types are not clearly distinct among the Pleistocene species.

Hipparion is a classic genus of the Pliocene of the Old and New World. It is distinguished from *Equus* by the separate protocone of the upper molars. A dozen or more valid species are known, three or four from the Pliocene, and uppermost Miocene of Europe, Asia and Africa, the rest from North America. All in which the skeleton is known retain complete lateral digits.

The species range from the size and

proportions of an ass down to those of a dorcas gazelle, and have a wide range also in the construction and proportions of the teeth. In some species the enamel of the lake borders is thrown into much more complex folds than in the horse, in others it is simpler. In some the protocone is round oval as in *Merychippus*, in others (subgenus *Neohipparion*) flattened as in *Equus*. One group of small American species (new subgenus *Nannippus*) has the teeth very long-crowned, up to a fourth longer than in any living horse; oval protocones and extremely slender limbs and feet, in which the side toes are complete but no trace remains of the fifth digit and trapezium. This group is typified by *Hipparion phlegon* of the Blanco formation, of which I secured skulls, feet etc. in 1924. Contrast it with the contemporary *Plesippus*, with stout limb and foot bones, the side toes reduced to splints but the trapezium and fifth digit still retained. Another group, mostly Old World species, typified by the well known *Hipparion gracile* of Pikermi and Samos, is comparatively large and robust with relatively stout limbs and feet and the side toes larger than they are in *Merychippus*. Most of the species have the lachrymal fossa in the side of the face deep and well defined, but in some it has disappeared almost completely.

The various species of *Hipparion* seem to have been trying out a variety of combinations of progressive features, carrying some of them further than *Equus* has done. They have in common the separate protocone and usually, if not always, the retention of the lateral digits. (The first is essentially a primitive character because it is caused by the commissure or connecting crest between protocone and protoloph remaining low or short, while the rest of the crown is elongating. It would seem to be a mechanical defect, making it easy for the protocone to break away from the rest of the tooth, except for the heavy coat of cement; but it is not a defect, for it did not prevent certain species from surpassing the horse in length of the teeth. Upgrowth of this commissure would convert the tooth in certain species into an *Equus* tooth, loss of the lateral digits into an *Equus* foot.)

The various American species grade back into *Merychippus*, from which *Hipparion* is clearly derived. In the Old World it appears as an invading type at the end of the Miocene (Pontian fauna).

Hippidium, a small group of South American horses, has exceptionally short legs, a curiously constructed nasal region in the skull, and teeth much like those of *Pliohippus*. They are of about the same bulk as the true horse. The free portion of the nasal bones is very long and slender, the notch between them and the maxillary bones extending far backward. This indicates I believe, not a proboscis as supposed by some writers, but a soft flexible structure behind the nostrils, prevented from collapsing by the slender nasal bone. Possibly it was analogous

FIG. 23. HIPPARION WHITNEYI. UPPER TEETH, TWO-THIRDS NATURAL SIZE. FROM A SKELETON, UPPER MIOCENE, SOUTH DAKOTA

to the curious face of the Saiga antelope, but its purpose and exact character are unknown. These animals, evidently descended from *Pliohippus* of the North American Pliocene, are known only in South America in the Pleistocene. The short legs were perhaps an adaptation to mountain habitat. Another South American Pleistocene genus, *Onohippidium*, has deep fossae or pockets in the side of the face in front of the orbits, as in many species of *Merychippus*, *Pliohippus* and *Hipparion*. It is otherwise much like *Hippidium* and probably of similar habits. *Hyperhippidium* or *Parahipparion* is even shorter legged and otherwise similar.

Anchitherium and *Hypohippus*. An older side branch is represented by a series of

FIG. 24. HYPOHIPPUS OSBORNI. UPPER TEETH, TWO-THIRDS NATURAL SIZE. MIDDLE MIOCENE OF COLORADO. AFTER OSBORN

species that begin in the Upper Oligocene with certain species of *Miohippus*, are continued by the Lower Miocene *Kalobatippus* and by *Hypohippus* of the later Miocene surviving to Lower Pliocene. This series retains the more primitive construction of the teeth with oblique crests and outer crescents, lengthening out crowns a little, and to some extent paralleling the rhinoceros adaptation of grinding teeth. The side toes also are persistently primitive, reduced progressively but more slowly than in the typical equines, and the hoofs are relatively large and splayed. Professor Osborn has designated this as the Forest Horse, and its adaptation is clearly to softer ground and more succulent food, although not apparently to forest life judging from its associations. These animals were larger than the contemporary stages of true equines, the last of them (*H. matthewi*) nearly as large as a modern horse.

This line invaded the Old World at the beginning of the Miocene, and is found in the Miocene formations of Europe and Asia until the end of the Miocene or beginning of the Pliocene. The name *Anchitherium* was given by Meyer to the European species, described nearly a century ago; and at one time, before the American Tertiary equines were known, *Anchitherium* was supposed to be in the direct ancestral line of the horse, linking it with *Palaeotherium*.

Archaeohippus. Closely related to *Parahippus*, and like it derived from *Miohippus*, this line remained small, short-crowned, and almost unchanged except for elongated face and deep facial fossæ. It is found in the Miocene. The skeleton so far as known is like that of the smaller species of *Parahippus*, of which it may be considered a subgenus.

DIVERGENT LINES LEADING TO TAPIR, RHINOCEROS AND OTHER TYPES

In the preceding pages have been reviewed a series of successive stages leading up from the little four-toed *Eohippus* to the modern horse. Each stage is found in its appropriate position in the geologic succession, never below or above its proper level (except for one or two

unaltered survivals noted in the review and indicated in the diagrams). A number of side branches leading up in similar manner to aberrant specialized Equidæ types now extinct have also been reviewed. We have now to review various races related to the horses but not included in the family, leading up in quite similar

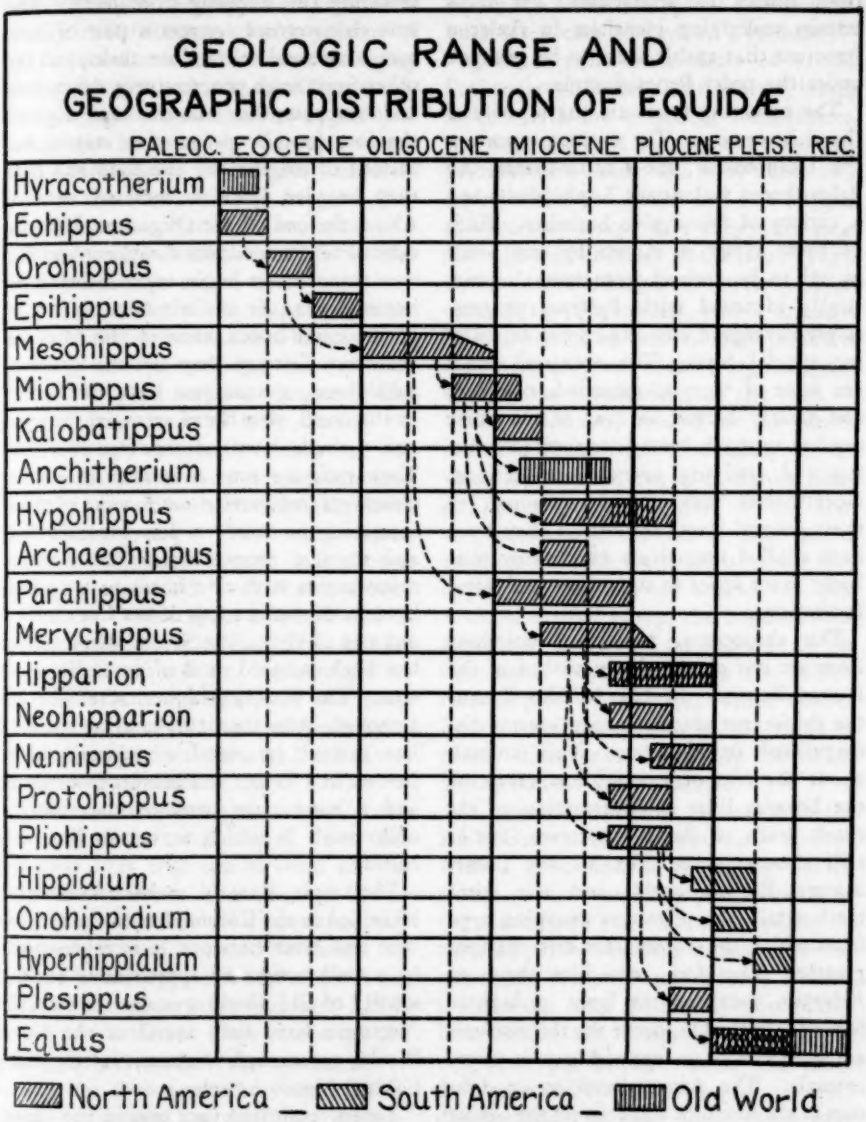

FIG. 25

fashion to a variety of specialized types, some living, others extinct, widely diverse from horses in appearance, yet with certain underlying identities in skeleton structure that enable them to be grouped under the order Perissodactyla.

The surviving types are the tapirs and the rhinoceroses. The extinct types are the Titanotheres, the Chalicotheres, the Palæotheres, Colodonts, Lophiodonts and a variety of minor side branches. Each of these types is shown by the fossil record to be derived from animals practically identical with *Eohippus* progressively divergent into their final or existing special form. The ancestral series are none of them so extended, complete and clearly defined as that of the horse nor has so much been done toward securing and studying adequate collections. Nevertheless they are clear enough in their general lines, and where they have been studied intensively they show similarly exact series in successive geological formations.

The rhinoceros, tapir and colodont lines are not clearly distinguished in the Lower Eocene. In the Middle Eocene the rhinoceros ancestry is first clearly distinguished in *Hyrachyus*. This animal, about the size of a wolf, has taken on the broader lines of construction of the cheek teeth of the rhinoceroses, but is still short-crowned like all the Lower Eocene Perissodactyls, and the front teeth retain the primitive cropping type from which the horses have not changed greatly. The feet are like those of *Eohippus*, four toes in front and three behind. In the Oligocene the rhinoceroses are more various in type and include larger animals. The Amynodonts retain four toes in the fore foot and convert the canine teeth into large tusks. The Hyracodonts reduce the toes to three on each foot, and like the horses begin to lengthen out the foot and reduce the side toes, also lengthening the crowns of the cheek teeth, but retaining the cropping front teeth. The true rhinoceroses convert a pair of incisors, above and below, into tusks, and the other front teeth progressively degenerate and disappear; they lose the outer digit of the fore foot by progressive stages, but instead of lengthening the limb and foot they broaden it with increase in size. About the end of the Oligocene, Hyracodonts and Amynodonts disappear and the true rhinoceroses begin experimenting on horns, first a pair of little nubs on the tip of the nasal bones, then in the Miocene and later Tertiary they try out a single nasal horn, a horn just back of the tip of the nasal, two horns arranged tandem, and a single horn on the frontal bone. They split up into a number of rather closely related parallel races, most of them increasing to more or less gigantic size and massive proportions. The African rhinoceroses with two horns have specialized further in the loss of the front teeth, and one of them, the White Rhinoceros, has high-crowned teeth of a peculiar pattern. The Woolly Rhinoceros of Siberia, although older than this existing species, has carried its trend of specialization further in a longer and heavier front horn and a bony crest between the nostrils underneath it which serves to brace it solidly.

The tapir line is rather doubtfully identified in the Eocene, but in the Oligocene and later horizons it is represented by a well recognized approximate series, mostly of Old World species. Few fossil specimens have been found in the New World, yet enough to show that they inhabited North America.

Tapirs retain the four toes in the front foot and three in the hind foot of the early Eocene Perissodactyls, and in many features of skeleton and teeth are very primi-

tive. The cropping incisors are retained, and the cheek teeth are still short-crowned, but the premolars are completely molariform, and the pattern of the molars altered to transverse chopping crests, the ectoloph almost disappeared. The progressive molarization of the premolars can be traced in the tapir stages from Oligocene to Pleistocene just as it can in the Eocene horse stages. One remarkable character is the evolution of a proboscis, also partly traceable in the Oligocene-Recent series.

The Titanotheres are an early extinct family of the Perissodactyls which specialized in giant size, retaining the four-three toes, developing massive rhinoceros-like proportions, a pair of long "horns" on the front of the skull, converting the molar pattern into two outer crescents and an inner pair of rounded cusps, the front teeth degenerating. These are common in the American Eocene and Lower Oligocene, and their evolution has been studied by Osborn from a splendid series of skulls and skeletons. The earliest stage, *Lambdotherium*, is closely related to the somewhat older *Eohippus*, and must have been derived from a predecessor which would be still nearer, but has not yet been discovered.

(Students of phylogeny whose attention has been concentrated upon the *differences* that will enable them to distinguish one stock from another in the early stages of their differentiation, may take exception to the above statement. A fair and honest appraisal of the characters of *Lambdotherium* as compared with *Eohippus* on one hand, and *Titanotherium* on the other, fully warrants the statement. I regard the over-emphasis of such differences, on account of their real or supposed phyletic importance, as gravely misleading.)

Intermediate between Titanotheres and horses are the Palæotheres of the Old World Eocene, much like the early equines in teeth, but robust and massive, with a tendency to develop a proboscis.

Another remarkable series of extinct Perissodactyls is the Chalicotheres, which in the teeth are very like Titanotheres, the skull and neck take on more the proportions of a horse, the body those of a tapir, while the limbs and feet suggest rhinoceroses except that they have large claws instead of hoofs on the toes. These have a record lasting from the early Oligocene to the Pleistocene, and a doubtful Middle Eocene ancestor of more primitive type with only the obscure beginnings of the various peculiarities of the race.

The Colodonts, related to the tapirs, and like them with a tendency to develop a proboscis, but with slender limbs and progressive elongation of the foot and reduction of the toes in some genera to three on each foot, are a group very imperfectly known or studied as yet. Another extinct group, the Lophiodonts, appears to be related on one side to the Colodonts, on the other to the Eocene rhinoceroses. Both groups are in need of further critical research in the light of recent discoveries, especially of Mongolian Eocene Perissodactyls.

In general it would appear that the Perissodactyls start in the early Eocene with a great number of closely related stocks, which specialize progressively in the successive Eocene horizons, partly on parallel, partly on divergent lines. These numerous branches are reduced by extinction one after another of most of the intermediate and competing lines, while the survivors became more and more divergent and specially adapted to their diverse modes of life. One branch may give rise to side specializations paralleling other branches, as the Hyracodont rhinoceroses and the Colodont tapirs parallel

FIG. 26 DIVERGENT EVOLUTION OF THE PERISSODACTYLS IN THE OLDER TERTIARY

The primitive group of hyracotheroids branches out during the Eocene into many phyla; separable in the Oligocene into four distinct groups through extinction of intermediate and synthetic types. During the later Tertiary these four groups continue their divergent specialization. Three still survive in the horses, tapirs and rhinoceroses; the chalicotheres became extinct in the Pleistocene.

the early horses, the Anchitheriine horses parallel the rhinoceroses (to some extent). Such parallelisms, of which numerous cases might be cited, sometimes succeed and displace the older specialized adaptation. In other cases (including the three cited) they fail, and become extinct. The explanation of such success or failure is to be found in the effectiveness of the type as an animal mechanism, in its physical environment encouraging or forbidding the expansion and survival of the adaptive type, and its biotic environment providing or excluding competitive types in the region.

It is not possible within the limits of this essay to discuss even in outline the interpretation of the various specializations from the primitive Perissodactyl stock; but in the next section I will attempt to outline the probable interpretation of the evolution of the Equid phylum.

MEANING OF THE CHANGE IN FEET AND TEETH. PROGRESSIVE ADAPTATION TO CHANGING ENVIRONMENT

In attempting to understand the causes of the progressive development of the Equidæ as preserved in the geologic record, we must first look to the physical changes in the region they inhabited. At the beginning of the Eocene the Western Plains region was very different from what it is today. It had but recently emerged from the sea, and was still much nearer sea level than now. The climate was milder and the rainfall much greater than now, so far as one can judge from the flora; and it was rather a region of forest and glade than of broad open plains. The environment was that of subtropical forested regions, and it is in such regions that one may find today the analogues as well as the nearest relatives of the Eocene mammals. *Eohippus* may be compared with the pudu of Central America and the tragulines of the Old World. It was probably a forest dweller, browsing on leaves and succulent herbage, the flexible four-toed foot adapted to the irregularities of the woods, to quick shifts and dodging behind covert, but not to speed over a uniform open surface.

During the Tertiary period there was a progressive rise of the great interior plains and cordilleran region, and change of climate. The rainfall became less, the tropical rain-forests retreated and the open glades expanded into broad grassy plains. Some of the animals, like the tapirs, retreated with the forests. Others, like the horses, adapted themselves to the new conditions. In great part the Evolution of the Horse is the record of this progressive adaptation.

The drier, harder grasses of the plains demanded more thorough triturition in order to make their food-values available. The change in the teeth is chiefly directed to the development of an efficient grinding apparatus for this purpose. This is secured, first by conversion of the premolars into molariform teeth, thus doubling the grinding surface, second through conversion of low, more or less rounded cusps into sharp crests and crescents, thus providing parallel shearing edges of enamel in the worn teeth as the lower jar sweeps across the surface of the upper in grinding the food. Next comes the elongation or heightening of the crowns of the teeth to prolong the life of this grinding apparatus. But with the elongation of this complex pattern of dentition it develops a weakness in the lack of support for the enamel, and a tendency to flake off, block the valleys and interfere with efficient grinding. This is obviated in Equidæ by development of cement, a softer material analogous to the dentine that is exposed inside the enamel, but deposited on the outside before the tooth cuts the gum. In the

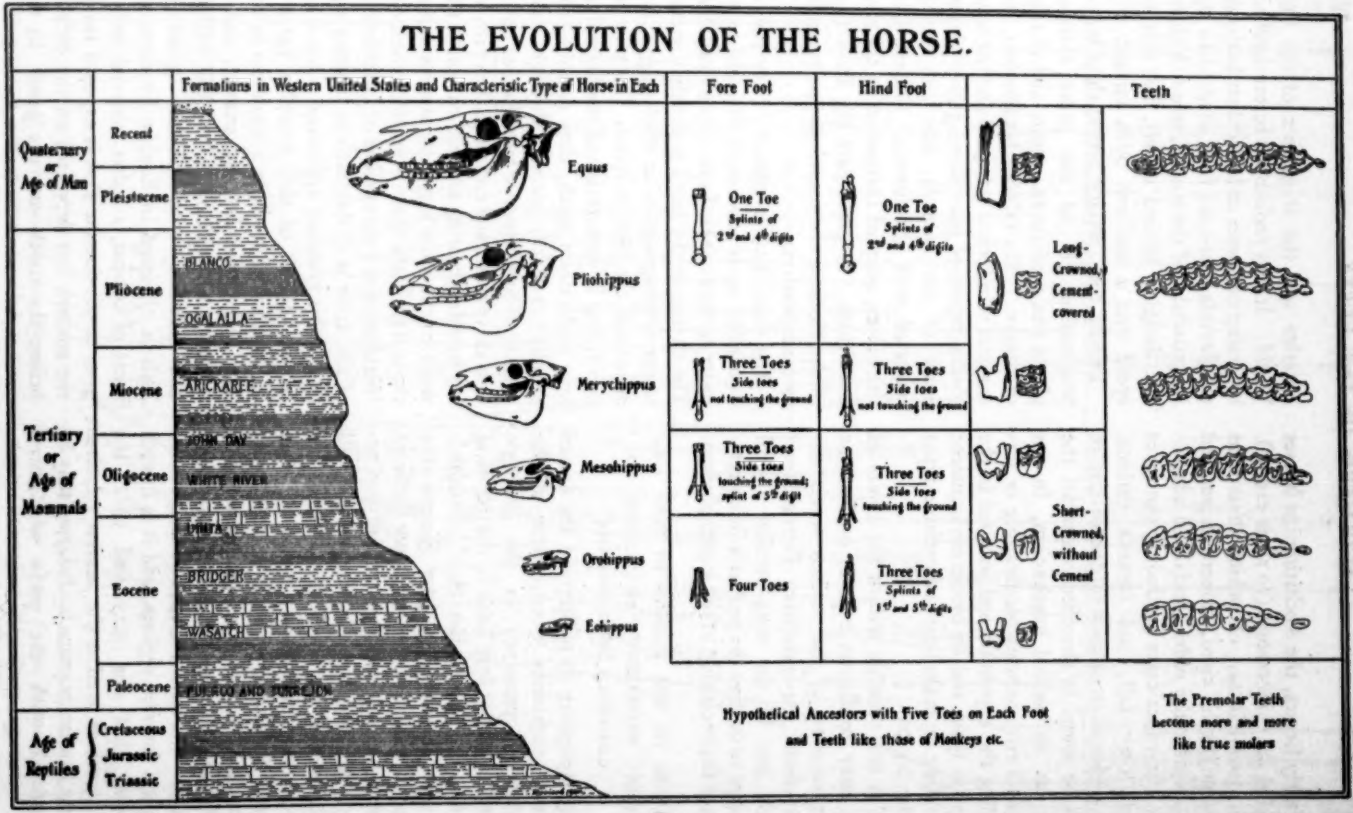
THE EVOLUTION OF THE HORSE.
Formations in Western United States and Characteristic Type of Horse in Each
Fore Foot
Hind Foot
Teeth
Quaternary or Age of Man
Recent
Pleistocene
Tertiary or Age of Mammals
Pliocene
Miocene
Oligocene
Eocene
Paleocene
Age of Reptiles
Cretaceous
Jurassic
Triassic
BLANCO
OGALALLA
ARICKAREE
JOHN DAY
WHITE RIVER
UINTA
BRIDGER
WASATCH
PUERCO AND TORREJON
Equus
Pliohippus
Merychippus
Mesohippus
Orohippus
Eohippus
One Toe
Splints of 2nd and 4th digits
Three Toes
Side toes not touching the ground
Three Toes
Side toes touching the ground; splint of 5th digit
Four Toes
One Toe
Splints of 2nd and 4th digits
Three Toes
Side toes not touching the ground
Three Toes
Side toes touching the ground
Three Toes
Splints of 1st and 5th digits
Long-Crowned, Cement-covered
Short-Crowned, without Cement
Hypothetical Ancestors with Five Toes on Each Foot and Teeth like those of Monkeys etc.
The Premolar Teeth become more and more like true molars

FIG. 27

modern horse the cement is deposited from fluids secreted by special glands (probably evolved during the later Tertiary from the salivary glands?). The development of cement, initiated in *Parahippus*, made possible a progressive elongation of the crown into a square prism which is pushed up from beneath as it wears off on the grinding surface, and might become in the further course of evolution rootless and continuous in its growth until the animal dies. This has occurred with various rodents; in the horse, however, the root of the tooth forms, and its *growth* ceases at about six years, after which it pushes upward in the jaw until it is completely worn down, when the animal can no longer chew his food and dies of malnutrition.

The change in limbs and feet is no less striking, and is equally explained as an adaptation to the progressively dry climate and open plains environment. Speed, especially long-distance speed, becomes essential to a defenseless herbivore living in open country. The plains surface is smooth and hard, and there is no need for flexible adaptable joints, or for side toes to adjust the step to an irregular surface. A long limb will cover more ground at each step, but if the proportions remain the same the step will be slower, as the normal swing of an animal's step is essentially a pendulum-swing. If the centre of gravity is shifted towards the upper part of the limb by lengthening its lower segments while shifting the muscles more into the upper part of the leg and moving the lower segments by long tendons, the length of step will be increased without decreasing the speed of its swing. Moreover, the reduction of the lateral digits and concentrating the step on a central digit will add to the speed by substituting a clean, quick drive from a tight-jointed, rigid hoof, for the soft, yielding push of the five-toed foot. These changes put a heavier strain on joints and ligaments, and these must be strengthened, the movements of the segments concentrated on the lines of locomotion at the expense of flexibility, by extending the fore-and-aft movements but limiting the lateral movements. Hence the deepening of the pulley of the astragalus, the shifting of wrist and ankle bones so that the inner and outer ones acquire a footing on the cannon bone, development of a keel at the end of the cannon bone, and a whole series of minor changes that can easily be seen to serve the same general purpose.

At the same time the tibia and fibula of the hind leg, the ulna and radius of the fore leg, originally two separate bones permitting considerable torsion at this joint, become more closely united, consolidate, and the shafts of the ulna and fibula become vestigial, the torsion of the joint wholly lost.

These limb changes involve changes in the proportions of the body and head. The neck and head must be lengthened out in order to enable the animal to graze. The barrel becomes shorter, deeper, less flexible, conformant with the limitation of the limb and foot movements, and again acquiring strength and speed at expense of flexibility.

A second series of changes in proportions and structure is related to increase in size. The advantage of increased size to an animal in competing with rivals or keeping off enemies is obvious enough, and up to a certain limit it results in increased speed. The disadvantage is based upon the well known engineering fact that the relative strength of a structure decreases with its size, as the strength is proportioned to the cross-section, but the weight to the mass. This is also true of the muscles; their strength is proportioned to

FIG. 27

their cross-section, their weight to their bulk. Hence, with increase in size the bulk of the animal increases as the cube of the linear dimensions, while the strength of the bones and muscles increases as the square of the linear dimensions. This must be offset by relative increase in the robustness of bones and massiveness of muscles. But the food requirements for the more massive muscles are also relatively increased, while the area covered in grazing increases with the larger animal only as the square of the linear dimensions. It results that larger animals need a good deal more food in proportion to their size, and, as a matter of observation, large animals spend a great portion of their time in feeding, while smaller animals can satisfy their relatively smaller food requirements in a small proportion of their time. This sets a limit to the size of an animal as a practical working mechanism, a limit that varies with the nature and abundance of the food and the perfection of the mechanism, and is affected by various other factors. (The more rapid metabolism necessary to maintain a constant high body temperature in a smaller animal affects the food requirements in an opposite sense to the above; but it is of less relative importance in mammals of the size here considered.)

The maximum of speed in a quadruped is reached at an earlier stage. Up to that stage the increase in size, although it involves a relative decrease in speed, enables the animal to cover more space within a limit of time. Beyond it, the greater massiveness necessary reduces the absolute speed. The swiftest living animals are of the size of the gazelles and smaller antelopes, and the three-toed horses of the later Miocene were probably swifter than their modern descendants. The larger animal, however, is more able to defend himself against enemies, and as long as his food is sufficiently abundant natural selection will develop races considerably beyond the point of maximum speed. This has happened with the horses, the larger antelopes and cattle and various other races. With all large animals, however, an adequate food supply is a relatively important factor in their survival, specialized habits become essential in order to secure sufficient food, and large animals are hence more liable to extinction through change of environment, and for other reasons which it would take too long to discuss.

We observe in the evolution of the horse a progressive elongation of the lower legs and feet, with disappearance of the side toes, and the various minor mechanical adjustments necessary to secure high speed. This reaches a maximum in the Miocene and Pliocene horses, and, in the Pleistocene and modern horses, especially the larger species have relatively shorter and more robust leg and foot bones. They have passed the speed maximum, and probably have reached the size maximum for that particular adaptation and environment. Modern horses are no larger than those of the Lower Pleistocene.

Many other changes in the construction and proportions of all parts of the skeleton have taken place *pari passu* with the changes cited. Most of them are obviously explained on the mechanical and adaptive principles outlined. The increase in brain capacity is a line of progress paralleled by most other successful races of mammals. It involves probably a great diversity of specialized adaptations of intelligence to the habits of the animal, but its real meaning can hardly be understood in the present state of our knowledge. The horse has undoubtedly developed a marvellous place-memory, and the special development of its brain has presumably centred largely on this

feature, conditioning the special pattern seen in the progressive complication of the convolutions.

The development and final degeneration of the facial pockets or preorbital fossæ is also an obscure point. Gregory (1920) has shown that these probably lodged diverticula of the nasal passages, but their function and usefulness is not known.

SIMILAR CHANGES IN OTHER ANIMAL GROUPS. PARALLEL ADAPTATION IN OTHER MAMMALS

If our explanation of the progressive changes in the Equidæ phylum is correct, we should find other animals doing the same thing. That is to say, other races of similar habits, subject to the same changes of environment, should parallel the Equidæ more or less closely. They should develop a superficial similarity, with underlying differences of construction that betray the different origin. Such we find to be the case. Among the great group of Artiodactyls (pigs, hippopotami, deer, antelopes, cattle, etc.) all the ruminants are seen in their geologic record losing the side toes, concentrating the step upon a central pair which become co-ossified into a "cannon bone" as in the horses, only with two hoofs instead of a single broad hoof. The teeth also become elongated with four crescents as in the horse, and in the cattle and some antelopes a large, high inner pillar on the molars and a heavy investment of cement make the molars singularly like those of horses. The premolar teeth, however, do not become like the molars; this deficiency in numbers of the grinders is offset by the habit of ruminating or chewing the cud.

In South America, in absence of true horses, another group of hoofed animals, the Litopterna, now wholly extinct, evolved a race which paralleled the horses in a very interesting way. They developed three-toed and one-toed types which resemble the true three-toed and one-toed horses superficially, but in details of construction are seen to be even more different than Tapir or Rhinoceros. Their teeth likewise resemble the teeth of the earlier three-toed horses, and likewise differ more widely in the underlying construction than do the diverse families of Perissodactyls of the north. (Yet these resemblances have been close enough to deceive able palæontologists in the past, when the evidence was more scanty than it is today.) When the true horses invaded South America in the Pliocene, these pseudo-horses became extinct. They had carried the specialization of the feet a stage further even than the modern horse, in one genus at least: *Thoatherium* has the side toes reduced to small nodules of bone; but this animal is quite small, about the size of a gazelle. Contemporary with it was a larger form, *Diadiaphorus*, with side toes reduced about as in the contemporary *Merychippus*. The teeth, however, are not beyond the stage reached in *Miohippus* of the Upper Oligocene.

THE BEARING OF THIS EVIDENCE ON EVOLUTION

In the preceding pages has been outlined a summary of the material facts of evidence in the case. The fossils, found in a certain sequence of geological formations, are the actual remains of animals that lived when that succession of formations was being deposited. They are a direct record of the geological history of the equine family, that is, of the animals anatomically related to the existing horses. There is no question about the succession of the formations; they have been traced across country, one overlying or overlapping another in such fashion that the sequence is certain. There is no

question that the various stages are found in their appropriate position in the geologic succession as recited above, and are found only within those limits as specified. This is proved by many thousands of specimens of the better known stages and by hundreds of nearly all the rarer stages, which have been found by various collecting parties during the last eighty years, especially during the last two decades, and are preserved in various museums, each with exact record of formation and locality in which it was found. Collectors have been keenly on the lookout for exceptions, for such exceptions would be of extraordinary interest to science; but they have not been found. Even certain *apparent* exceptions when more carefully studied have been found not to be real exceptions.

Broadly speaking, the evolution of the horse in the sense of a regular progression by gradual stages from small primitive four-toed ancestors to the large, highly specialized, one-toed horse, appears not as a theory but a fact of record. It is equally a fact of record that the tapir and rhinoceros are derived from the same primitive stock through a similar series of progressive stages. Widely different in appearance and habits today, they have diverged from a common ancestral stock.

If, therefore, we turn to the record of geologic history to answer the question whether as a matter of fact the diverse types of existing animals did evolve from common primitive stocks, or whether the various races have remained unchanged since they were created, the answer is perfectly definite and categorical. Whenever the evidence is sufficient, as it is in this instance, it proves the theory to be a fact of record. When the evidence is insufficient for proof, it fits in with the evolution theory, so far as it goes. It is in comparatively few instances out of the millions of existing species that the categorical proof of their evolution is at hand. This will always be true, although the number of proofs and the completeness of the evidence grows year by year.

It is asserted by some opponents of evolution that "the evidence is all circumstantial." Probably what they mean is the anatomical evidence—which, moreover, they totally misconceive in saying that it is "a matter of resemblances." The fossil evidence, however, is not circumstantial; it is the direct testimony of the record itself, far better than "eye-witness testimony," for eye-witnesses may easily be mistaken, and often are, and there is no way to discover and correct their mistakes save the imperfect and uncertain methods of collation and cross-examination. As for the evidence of comparative anatomy, while it is indirect, and may be compared to circumstantial evidence, its weight lies not at all in "resemblances" but in identity of structural plan underlying a wide *diversity* of appearance and habits. We regard horse and man as related, not because they resemble each other, for they are utterly diverse in appearance, but because in spite of this diversity the anatomist finds that their underlying structure is fundamentally the same.

The causes and methods of the evolutionary process are matters of theory. The fossil record throws much light upon some of the problems involved; others are wholly outside of its field. From detailed study of abundant material within a limited portion of the record, the range of individual variation of the animals in a certain area can be followed through the considerable period represented by a fossiliferous formation or succession of formations. Whether or to what extent these lie in genetic descent is a matter of relative probability, not of direct evidence.

Migration, the continuous shifting of range and species, invading new regions and abandoning old habitats, must always play a part, probably a dominant part, in the making of such a record. The gaps or apparently sudden jumps in a well documented phylogeny often ascribed to "mutation" are, in most cases, due rather to migration. This much can be said, that the more complete the record, the more abundant the material, and the nearer we are, judging from the available evidence, to the probable centre of evolution and dispersal of any race of animals, the more continuous does the succession become, the more it appears to evolve through a succession of minute changes which lie within the limits of ordinary individual variation.

For the facts as to the nature and kinds of individual variations and the laws of their inheritance or non-inheritance, the palæontologist must turn to the geneticist. But it is apparent that the large and obvious "mutations" which the geneticists select for "experimental evolution" have not played any part in natural evolution as observed by palæontologists. Probably the same laws of inheritance which they have deduced from the study of these large "mutations" apply equally to the minute and very frequent heritable variations whose existence in ourselves and familiar animals has always been a matter of common knowledge. It is equally true of fossil animals, that no two are exactly alike, equally probable *a priori* that the variations are partly heritable, partly non-heritable, and that heritable variations are acted upon by natural selection. Some geneticists have shown us why such variations cannot accumulate into diversity of species and genera; but the palæontological record shows that they do, and the fallacy that lies behind the geneticists' argument is not difficult to discover.

This fallacy turns partly upon a feature of natural as against artificial selection that it is not easy for a zoölogist to appreciate, namely, the exceeding slowness of evolutionary changes in nature, and the vast length of geologic time. The Pleistocene period covers, according to recent estimates, more than a million years, more, that is to say, than a hundred thousand generations. Yet the amount of change in the horse phylum during that time is measured by the difference between one species and another. Artificial breeding produces in a hundred generations corresponding or greater changes in certain parts, but then comes against an apparent barrier to further change because the heritable variations necessary to accumulate further changes and coordinate them with other parts of the mechanism are not potentially available in the limited numbers of the stocks used for breeding. But in nature the stocks are not so limited; they consist of many millions of individuals scattered over one or several continents, and intermingled and crossed through the shifting of range and migration over a period a thousand times as long. If we assume that new heritable variations appear from time to time in the heredity of each herd—and common knowledge of the heredity of our own species makes this appear rather as observation than assumption—the number of potential variations available for breeding will be quite limited in dealing with a single herd over a few generations, but practically unlimited in natural selection through geologic time.

Now any wide departure from the normal in an individual is not advantageous because it interferes with the effectiveness of the animal as a working mechanism, and cannot be adjusted by numerous other changes of corresponding amount necessary in order to make the machinery work effectively.

To amputate the side toes from a dog would cripple it, not help it, because the central pair are not strengthened, the muscles are not adjusted to the new conditions, a hundred other correlated changes are not present. On the other hand, a slight change, a little elongation of the limbs or feet can be, and is normally, adjusted through the growth of the animal. These adjustments are not inherited; they cannot accumulate. So that while the heritable difference can accumulate, it soon reaches a point where the necessary co-ordinations are too great to be made through adjustments during the growth of the individual, the further evolution of the character ceases to be of advantage because it becomes a mal-adjusted mechanism, and until heritable variations can be introduced into the heredity to replace these non-heritable adjustments, no further progress can be made. Time and intercrossing will finally overcome this lack; it is a brake on evolutionary progress, not a barrier, but it may explain why the record shows evolution to progress with such extreme slowness. The palæontologist has indeed a different scale; he often speaks of rapid evolution and even of "explosions" of phyla. But an explosion which took at the least many thousands of centuries to explode would not seem to the lay mind to be so very sudden; and in fact I doubt whether there is any real evidence of more rapid evolution than the change from *Eohippus* to *Equus*, and that, if the radium calculations are correct, took some fifty million years. It covers ten intermediate generic stages, and, if we assume that valid species are one-tenth as far apart as valid genera, we would figure that it took on the average five hundred thousand years to change from one species to the next in descent. The palæontologist, accustomed to his astronomical time-scale, may speak of the extremely rapid evolution of Tertiary mammals in contrast to the (relative) fixity of the turtles and crocodiles—but what he means by "extremely rapid" is a barely perceptible mutation in half a million years. (Barely distinguishable, that is to say, from mere individual variation. The quotation is from Osborn's recent address "The Origin of the Species as Revealed by Vertebrate Palaeontology.")

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RECENT RESULTS RELATING TO CHROMOSOMES AND GENETICS

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THE success of the method of interpreting genetic results in terms of a chromosome mechanism must be apparent to any one who has followed the literature of recent years. This is not only true of the mechanism as applied to Mendel's law of heredity, but also to many of the novel situations that are continually presenting themselves where a strict, and in some cases even a predictable, parallel has been found between new genetic occurrences and an alteration in the chromosomal mechanism.

In the following pages three lines of recent advance will be discussed; first, the evidence relating to an increase in chromosome number and its bearing on the problem of a permanent change in the number of the chromosomes; second, the evidence of sex-chromosomes in dioecious plants, and the interpretation of sex in terms of genes; third, the evidence relating to the "emptiness" of the Y-chromosome.

MULTIPLE CHROMOSOME GROUPS

Recent discoveries have shown that species belonging to the same genus sometimes differ from each other in that their chromosome numbers are multiples of some basal number which is the gametic or haploid number of the lowest member of the series. It is tempting to interpret these polyploid series as having arisen by the doubling, trebling, quadrupling, etc., of the number of chromosomes. There can be no doubt but that this is the correct interpretation in particular cases, but the observations have now gone far enough to show that it is unsafe to reconstruct all polyploid series on the assumption that they have arisen in this way. When the evidence from pedigree cultures suffices to show that a fourfold type has arisen directly from a diploid type, there can be no doubt but that the same set of chromosomes is present in fourfold number in the tetraploid, but without this direct evidence it is unsafe to conclude that a double chromosome type of one species has necessarily arisen from a related species by a direct process of doubling.

The characters shown by those diploids, triploids, tetraploids, that have arisen in pedigree cultures may be ascribed to the differences in their chromosome numbers, but when the differences in numbers have come about in other ways, as by hybridizing, for instance, the situation is more complex, and the characters may be due, in part, to the differences in the number of the chromosomes and in part, to the combined effects of the chromosomes of different kinds brought together in the hybrid. The problem is further complicated by the relative volumes of the cytoplasm in cells with different numbers of chromosomes, since this involves questions relating to the influence of the chromosomes on the amount of protoplasm present in the cells, and the subsequent effect of the chromosomes on this amount.

These considerations are not merely *a priori* possibilities but have arisen in connection with recent work on chromosome numbers and have been much discussed in recent literature of genetics and cytology. For example, there can be little doubt that the differences in characters between the diploid and tetraploid evening primrose are primarily due to differences in chromosome numbers. The same statement may be made for the diploid and tetraploid *Daturas* and for the diploid and tetraploid tomato and nightshade. In the polyploid series of roses that have recently been studied by Täckholm, by Harrison and Blackburn and by Hurst, there is evidence that some of the polyploids may be multiples of a basal type, while in other cases, there is evidence from the characters of the roses themselves, as well as from the behavior of their chromosomes at the maturation divisions, that the increase in number of chromosomes may have come about through crossing between different species. Hurst in particular has brought forward evidence in support of his view that five distinct varieties (or species) are at present combined in different ways in the roses of the Canina section. This evidence is so interesting that a somewhat more detailed statement may be given.

Hurst thinks that the Canina roses can be referred to five primary groups or species that are now combined as tetraploids, hexaploids, octoploids, etc. These polyploids, he thinks, are not to be regarded as multiples of the primary types, but rather as composite forms produced perhaps by hybridization. It is true that Hurst finds certain geographical difficulties in ascribing a hybrid origin to these roses, and suggests that the lower numbers of the series with fewer chromosomes have arisen through the loss of groups of 7 chromosomes each, but this interpretation is difficult to bring into line with the known behavior of chromosomes in the maturation divisions of eggs and sperm. On the other hand, other evidence from the work of Harrison and Blackburn and from the cytological evidence by Täckholm indicates, that some of the polyploid roses have arisen by doubling of a basal set of chromosomes. For instance, Täckholm finds that the smallest number, present in some species, is 14 (diploid) chromosomes. There are others that are tetraploids (28), others hexaploids (42), and others that are octoploids (56). Some of these groups are represented in figure 1. In those cases where the increase in numbers has arisen directly by doubling or quadrupling the diploid number, it is to be anticipated that at the time of conjugation of the chromosomes each chromosome will find a mate (or else like chromosomes will mate in fours) and consequently at the reduction division they will separate and pass to opposite poles leaving no unmated, "single" or lagging chromosomes on the spindle. Those roses whose chromosomes are in pairs in the maturation stages (of the pollen) are interpreted by Täckholm as having arisen by doubling. On the other hand the maturation divisions of other roses give a different picture. For instance, seven chromosomes may pair with seven, leaving fourteen unpaired (single) chromosomes lagging on the spindle. The simplest interpretation in such cases is that the fourteen single chromosomes have had a different origin from the fourteen that conjugate. In other species there may be again seven paired and in addition twenty-one singles, and in still others seven paired and twenty-eight singles, etc. It seems not unreasonable to suppose that the fourteen chromosomes that conjugate to give seven pairs are in all

cases members of one species, while the additional 14 or 21 or 28 have come from another species and have been brought together through hybridizing. If this is the correct interpretation, polyploid species may arise within the same genus either by doubling, quadrupling, etc. of the same set of chromosomes, or by the addition of foreign sets.

It is clear that an understanding of these relations must have an important bearing on the genetics of these roses when these combinations have been further worked out.

himself points out, the chromosomes, even in species having the same number, may have different size relations, and the nuclear diameters (resting stages) do not always bear a constant relation to the number of chromosomes present.

In different species of clovers (*Trifolium*) the following chromosome numbers (diploid) have been recently reported by Karpetschenko. Eight species have 14 (fig. 2), eleven have 16, one has 32, one has 48, one has about 80, one has about 130. If the haploid number be taken as eight, then four of the series are multi-

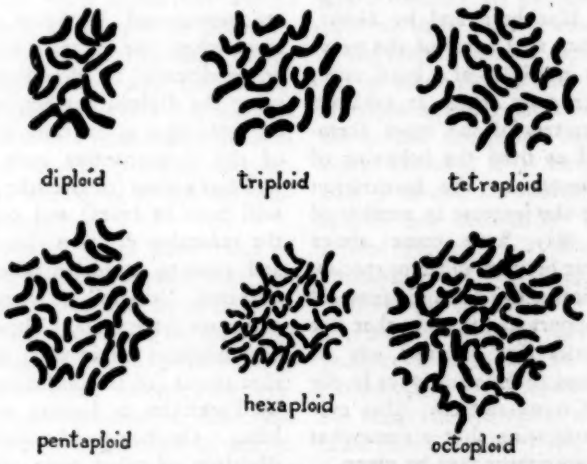

FIG. 1. CHROMOSOME GROUPS FROM DIPLOID CELLS OF DIFFERENT SPECIES OF ROSES
(After Täckholm)

The danger of erroneously interpreting all polyploid series in terms of multiples of a basal chromosomal number is also obvious when other groups of species are considered, in which, while some forms may be ranged as multiples of an assumed basal number, others are just as obviously not such multiples. A few such instances may be cited by way of illustration. In the cultivated varieties of chrysanthemum, Tahara finds varieties with 9, 18, 27, 36 and 45 chromosomes, but as he

ples of this number, namely 16, 32, 48, 80. The highest number (130) is only approximately correct, if it had two less (128) or six more (136) it would fall into the series. The smallest number (14) that is present, in about one-third of the series, stands apart from the rest of the species. It could arbitrarily be derived from the 16 type by the union of two chromosomes, or the 16 type could be derived from the 14 type by the breaking apart of two chromosomes of the latter,

but there is nothing in the sizes or shapes of the chromosomes to warrant this assumption. Bleier has also recently made a study of chromosome numbers in several species of clovers. Four species examined by him had 14, eight species had 16, one species had 18, two species had 28, two had 96–98. In this account the numbers 14, 28 and 98 (?) might possibly be interpreted as multiples of 7, while 16 and 96 (?) might be interpreted as multiples of eight. Taking Karpetschenko's and Bleier's results together, assuming the numbers to be substantially correct

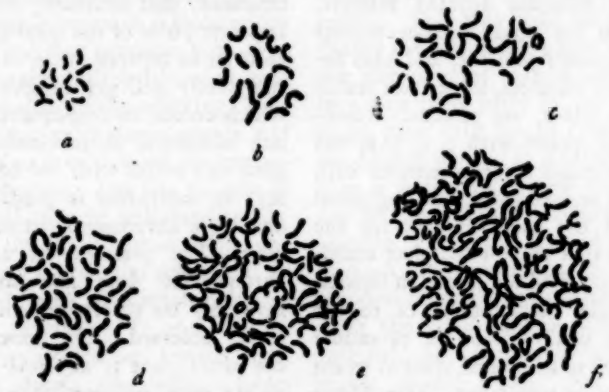

FIG. 2. CHROMOSOME GROUPS OF SOMATIC CELLS OF DIFFERENT SPECIES OF CLOVERS (TRIFOLIUM) WITH 14, 16, 32, 48, 80, AND 130 CHROMOSOMES
(After Karpetschenko)

(they do not always agree), a case for two series, multiples of 7 and 8 respectively, might be made out, but there are several further considerations that make such a generalization of doubtful value. For instance, Bleier, who has studied especially the reduced groups (gemini) points out that while, in some species the number and size of the chromosomes may be the same, in other species, the number of chromosomes may be the same but their sizes different. A comparison of still other species shows that while the number of the chromosomes as well as the size in one species may be double that of another species, in other cases, the number may be doubled but the size remains the same, or the number as well as the size of the chromosomes may be six or seven fold as great. It is evident, as Bleier points out, that from these relations the differences in numbers must sometimes have arisen in different ways.

Heilborn also sounds a note of warning against the arbitrary arrangement of chromosome numbers in series of multiples in a phylogenetic sense. In the sedges, *Carex*, there are many differences in chromosome numbers. For example, it is possible to pick out species that may appear to have chromosome numbers that are multiples of three as a fundamental haploid number, thus 9, 15, 24, 27, 36, and 42 chromosomes. It is also possible to put together a series that has four as a fundamental number, thus 16, 24, 28, 32, 36, 40, and 56 chromosomes and still others that are multiples of seven, thus 28, 35, 42, and 56. Several of these numbers appear in two or more of the series. Furthermore the size relations in certain cases are not consistent with the assumption

that the higher numbers are simple multiples of the lower. There can be little doubt that the solution of the problem can not be found in such a simple fashion. That polyploidy may in some cases play a rôle in the production of the hybrid numbers of chromosomes can scarcely be denied, but that all cases of multiples are in themselves evidence of polyploidy is clearly not true. Other evidence of a different sort will be required in each case before it can be interpreted in relation to the others. The genus *Crepis* is one of the earliest in the plant series whose chromosome numbers aroused interest, both because the small number present made exact counts possible, and also because different numbers, sometimes multiples of each other, are present. Rosenberg recorded species with 3, 4, 5, 8, and 20 pairs. Marchal recorded species with 3, 4, 5, 6, 8 and 16 pairs, and suggested that four is the basal number for the group; those that are not complete multiples being accounted for as due to bipartition of single chromosomes or to the doubling of certain pairs—a procedure that has come to be looked upon in recent years with some scepticism. Miss Mann has recently reported one species of *Crepis* with 6 chromosomes (n = 3), seventeen with 8 chromosomes (n = 4), five species with 10 (n = 5); one with 16 (n = 8); one with 18 (n = 9), and one with 40 (n = 20). While a basal number four will serve for some of these species, other species are not multiples of this number. Measurements of the chromosomes of several species, that have been made by Miss Mann, do not give much further insight into the possible interrelationships between the chromosomes in this genus.

THE ADDITION OF SINGLE CHROMOSOMES

In most animals and plants the diploid or double number consists of pairs and is therefore an even number. The exceptions to this rule are those cases where one sex has one less chromosome than the other. On rare occasions an additional member of one pair may appear giving three of a kind. These are called trisomic or triplotypic forms. The first case of the kind was observed in *Oenothera*, where 15 chromosome plants were found. Later, other cases were recorded, for example, in *Drosophila* and in *Datura*. The way in which such a condition is reached is fairly well understood. At the maturation of a germ cell, two daughter chromosomes, that ordinarily would pass to opposite poles of the mitotic spindle and then go to separate cells, fail to separate completely and get caught in one cell, which comes, in consequence, to contain one additional chromosome. If such a germ cell unites with one of the opposite sex, an individual is produced that has one more chromosome than the normal type. The presence of an additional chromosome does not appear to act favorably on the individual in the cases so far observed. The normal balance of the genes, that is adjusted to produce a viable type, is upset with more or less serious results. The evidence, as far as it goes, does not seem favorable, therefore, to the view that new self-perpetuating types could be established in this way. Moreover such heteroploid types, when bred to the normal type, transmit their combination to only half of the offspring. The chance is, therefore, that in time they would be eliminated on both counts.

There is, however, something further to be said in this connection. If the extra chromosome in question is a small one, like the fourth chromosome of *Drosophila*, the balance may be little disturbed and the characters little affected. In other cases, where a larger number of chromosomes than in *Drosophila* is present, the

addition of one new member may also be less injurious. Moreover if polyploidy has already taken place the addition of a new member might less seriously affect the viability since the balance of the genes is less disturbed.

The occurrence of a type with one additional chromosome furnishes theoretically the possibility of producing from it a type with two additional chromosomes, i.e., four of one kind, or a tetratype or tetrasomic type. Such a type, other things being equal, might seem to give an opportunity to produce a new type with an additional pair of chromosomes. If the tetrasomic type belongs to a monoecious species, i.e., one that produces both eggs and pollen grains, self-fertilization will give, in one-fourth of the offspring, individuals with two extra chromosomes, and there will be an even number of chromosomes to conjugate. But the balance of the genes will then be still further disturbed than in the trisomic type, and the expectation is that the result will be more injurious even than when only one chromosome is added. In the few instances of the sort that are known, viz., *Oenothera* and *Datura*, the evidence gives little encouragement for the view that, by the addition of two extra chromosomes, new types may be established.

The loss of a member of a pair of chromosomes also produces an uneven number of chromosomes. Such a result may be more injurious to the individual than the addition of one chromosome, and if, through such a condition, the further loss of the other member of the pair results, which is theoretically possible, the evidence indicates that the effect will generally be fatal to the life of the individual. Thus while the loss of one of the smallest chromosomes of *Drosophila* can be borne the loss of both small chromosomes seems to be fatal. At least, no such individuals have as yet been found under conditions that would lead to the formation of such combinations, namely, by mating two individuals each with only one of the fourth chromosomes.

There remains for consideration the possibility that an increase in the number of chromosomes may come about through the breaking apart of one or more chromosomes. In fact there are numerous cases on record where broken chromosomes have been detected in cells, and other cases where one or even all the chromosomes may break apart as a regular procedure. This may seem to give a better chance for establishing new numbers. If one chromosome should become broken into two parts early in the germ track, many germ cells might come to contain the broken parts. In a monoecious plant that is self-fertile, a new individual arising by the union of two such cells would contain four pieces, instead of the usual two chromosomes, and if these pieces behaved normally in division, a new type with the same number of genes as the original, but with two more chromosomes, would result. But there is an obvious objection to such a simple solution. The chromosomes are attached to the poles of the spindle by achromatic fibres that arise from or are connected with specific regions of each chromosome. It is uncertain whether both pieces of a broken chromosome could move (or be carried) to the poles of the spindle as do normal chromosomes. At least, until evidence on this score is available, it is hazardous to build up a theory on the assumption that cell division would be normal.

The problem is even more complex in forms with separate sexes where the broken chromosome pieces would have to be carried along through successive gen-

erations until like met like—an improbable, although a possible event. Since no advantage is supposed to arise from the separation, and possibly some disadvantage in mitosis, as stated above, it does not seem likely that such a condition would be self-perpetuating.

There remains another possibility, namely, that a bent chromosome might break apart at the attachment point of the spindle fibre and each part might then possess a spindle-fibre attachment of its own. This might seem more probable if the bent chromosome had been formed by a previous union of two chromosomes uniting at their spindle-fibre ends. In fact, there is one known case in which two chromosomes (with known mutant genes) became attached to each other. On rare occasions the two may again separate and then one part at least is known to behave as a normal single chromosome. The case referred to is that of *Drosophila* in which on four occasions the two straight X-chromosomes became united at one end to form a V-shaped chromosome. This process, to be sure, does not give a type with one less chromosome, since the two united chromosomes take the place of the two single ones in the female, and the male then gets his single X from his father. The two united X's may break apart, and usually at the point of union. Here we have proof that union and separation of two chromosomes may take place, but the situation is unique and its general application may seem doubtful. Nevertheless the result invites a comparison between the shapes of the chromosomes in different species of *Drosophila* where some species have two pairs of straight rods that may be, and have been, in fact, compared with a single pair of bent chromosomes of other species. Metz has brought together in a diagram (fig. 3) the diploid chromosome groups of

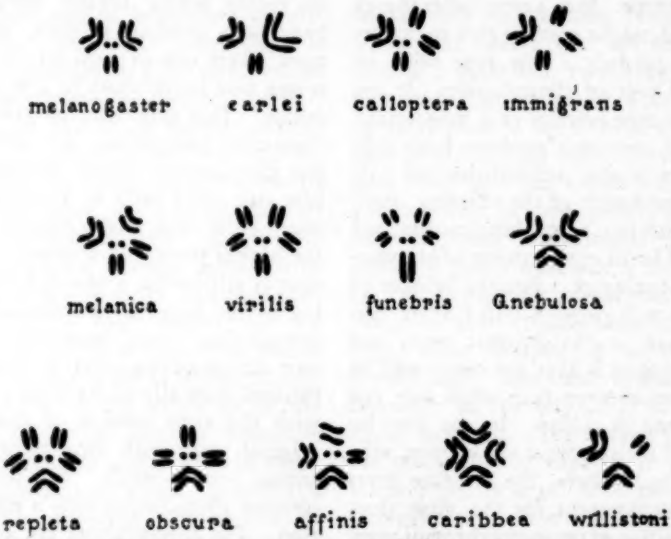

FIG. 3. DIAGRAM OF FEMALE CHROMOSOME GROUPS (DIPLOID) OF DIFFERENT SPECIES OF DROSOPHILA; THE PAIR OF X-CHROMOSOMES IS THE LOWERMOST PAIR IN EACH GROUP

(After Metz and Moses)

different species of Drosophilidae. Inspection of these groups will show how easily some of them may be converted into others by supposing that two pairs of chromosomes have united, or contrariwise by supposing that a pair has become separated into two pairs. It is

FIG. 4. DIAGRAM OF MALE CHROMOSOME GROUPS OF DROSOPHILA MULLERI AND D. REPLETA
(After Metz and Moses)

quite possible that this is the explanation in some cases, but the risk involved in any such arbitrary procedure may be illustrated by a single instance from the figures given. Two species, *Drosophila repleta* and *D. mulleri* are so closely alike that they "were reared in the laboratory under the same name until it was found that they differed in their chromosomes and that they would not hybridize." Subsequently they were differentiated by several external characters. Both species have the same number of chromosomes (fig. 4) but in *repleta* the X-chromosome is bent and in *mulleri* it is straight. In the former the bent X is about twice as long as the straight X in the latter. If the bent X's be supposed to have arisen by the union of an X chromosome with an autosome, it is not apparent where such an autosome could have come from since the same number of autosomes is present in both species.

Delaunay has recently made direct comparison between species of plants belonging to the two genera *Bellevalia* and *Muscari*. In the former there are in some species eight chromosomes each sharply bent giving a longer and a shorter arm (fig. 5). In the latter there are species with sixteen straight chromosomes whose sizes seem to correspond to the parts of the bent chromosomes of the *Bellevalia* group. Delaunay thinks that the transition from one genus to the other is brought about by the simple process of separation of the bent chromosomes into their component parts, but from the point of view of the genes it is not apparent how a simple separation could be the immediate cause of the change in the character of the plants, nor does it seem probable that such a separation would occur simultaneously in all the bent chromosomes at the same time. Granting that the two chromosome groups may, in some of the species at least, bear the interpretation that Delaunay has put upon them, it may appear that other change and perhaps changes in genes may be the more immediate cause of the differences in the characters of the different species.

FIG. 5. BENT CHROMOSOMES OF BELLEVALIA (ABOVE TO LEFT) AND OF MUSCARI (BELOW)
The first two flowers to the right are *Muscari*, the second two are *Bellevalia*. (After Delaunay)

THE ESTABLISHMENT OF NEW CHROMOSOME NUMBERS BY HYBRIDIZING

Another way in which types with new chromosome numbers may at times arise

is indicated by the recent work of Ljungdahl, and of Clausen and Goodspeed, who have produced, by crossing, types with stable chromosome numbers different from the original parental ones and multiples of a basal number common to those types. A poppy, *Papaver nudicale*, having 14 chromosomes (n = 7) was crossed to *P. striatocarpum* having 70 chromosomes (n=35). The hybrid has 42 chromosomes (fig. 6) and is fertile. When its germ cells mature there are 21 paired chromosomes (gemini), that separate at the first division (fig. 6*d*), 21 passing to each cell. No single chromosomes and no irregularities are present. A new type, a hexaploid, with 42 chromosomes has been produced. By backcrossing such a type to one of the parental types it may be possible to produce tetraploid, and octoploid types.

Whether the poppies used in this cross are to be ranked as varieties or species is uncertain, but it is evident that since one type brings in only seven chromosomes, and since there are twenty-one conjugants in the hybrid, some of the pairs must be made by union of the chromosomes of one type with those of the other, while the remaining conjugants must be formed by the union of chromosomes from the parent with the larger number.

Another remarkable case has recently been reported by Clausen and Goodspeed in which a stable type with a new number of chromosomes has been formed from

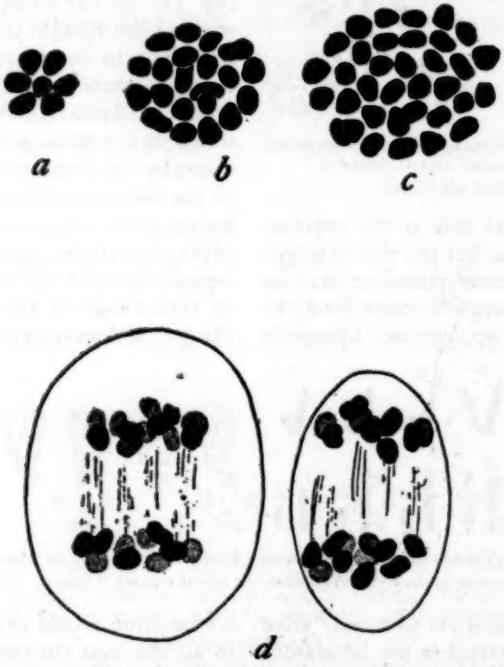

FIG. 6. *a*, CHROMOSOME GROUP (GEMINI) OF PAPAVER NUDICALE WITH SEVEN GEMINI (DIPLOID 14); *b*, OF P. STRIATOCARPUM WITH 35 GEMINI (DIPLOID 70), AND *c*, OF HYBRID WITH 21 GEMINI (DIPLOID 42) Below are two sections of the same dividing sperm-mother-cell without any lagging chromosomes. (After Ljungdahl.)

two undoubted species of tobacco. The two species *Nicotiana glutinosa* and *Tabacum* generally give, when crossed, a weak hybrid that produces only a few viable seeds after self-fertilization. Three such hybrids were obtained, one of which was partially fertile after hand-pollination. It produced numerous F_2 offspring, most of which were fairly fertile. One of the F_2 plants was more robust than the others. When its chromosomes were studied, 36 bivalents were found to be present. The somatic number, therefore, must be 72 which is exactly twice the number (36) present in the first generation (F_1) hybrids formed by the union of 12 chromosomes from *glutinosa* and 24 from *Tabacum*. The result may be interpreted to mean that a doubling of all the chromosomes had occurred immediately after fertilization in one of the F_1 hybrids. Such an occurrence would bring about a diploid condition in each set of chromosomes, and hence a composite tetraploid with respect to the sum total of its chromosomes. The new type then, contained 24 *glutinosa* chromosomes (12 + 12) and also 48 *Tabacum* chromosomes (24 + 24). There would be expected to be present in the maturation stages of this F_1 plant two of each kind of chromosomes, which, mating in pairs, would give the recorded number of 36 bivalents. The observed regularity of the reduction division in this tetraploid hybrid is in accordance with this view, especially when contrasted with the irregularities observed in the ordinary F_1 individuals having 36 chromosomes where there are numerous unpaired chromosomes that are distributed irregularly.

Thus a new hybrid type with a new chromosome number, that is expected to breed true to its hybrid characteristics, has been produced from a cross of two undoubted species. Clausen and Goodspeed point out that the same explanation may be applicable to the tetraploid *Primula kewensis*, a hybrid of *P. floribunda* and *P. verticillata*. The original hybrid was sterile but it produced a bud sport that gave rise to the constant form known as *P. kewensis*. Each of the original species had 18 chromosomes (haploid 9): the sterile hybrid had 18, and *P. kewensis* 36 chromosomes. The latter may be supposed to have arisen by a somatic doubling of the 18 chromosomes present in the hybrid, and as a result there would be two of each of the original kinds of chromosomes in the bud sport that gave rise to *P. kewensis*. It is, then, a hybrid tetraploid breeding true to its double chromosome composition.

SEX AND SEX CHROMOSOMES IN FLOWERING PLANTS

The recent discovery of a pair of differential sex chromosomes in several dioecious flowering plants has aroused much interest. In animals the main facts connected with the sex mechanism are well known and a review of the evidence is unnecessary, but in plants the facts are so new that a brief summary of recent work may not be out of place.

The simultaneous announcement in 1923 by three independent investigators that a differential pair of chromosomes occurs in certain dioecious plants came as a surprise because sex chromosomes had been often looked for in plants but not discovered. Santos examined the dioecious plant *Elodea* and found in the male an unequal XY pair of chromosomes (figs. 7 and 8) besides the 44 autosomes. Two kinds of pollen grains result, one with X (and 22 autosomes) the other with Y (and 22 autosomes). The chromosomes of the female were at that time not recorded but the occurrence of an unequal pair in the male plant and their segregation in different gametes made

their interpretation as sex chromosomes very probable. A year later (1924) Santos reported a pair of sex chromosomes in the female of *Elodea* that were equal in size (fig. 8) and corresponded to the larger member (X) of the XY pair in the male. opposite pole. This was confirmed a year later by Sinoto ('24). Two kinds of pollen grains result, presumably sex differentiating. Another botanist, Winge, reported at the same time an unequal pair of chromosomes in the male hop-plant

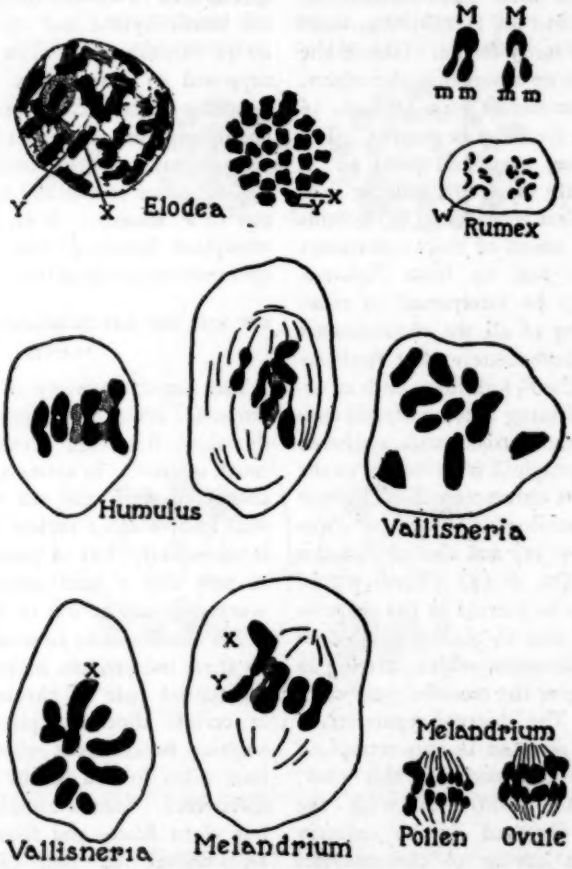

FIG. 7. SEX CHROMOSOMES (X AND Y) IN SEVERAL DIOECIOUS FLOWERING PLANTS (After Belăr)

Two cytologists, Kihara and Ono have found two small chromosomes and one large one in the male of *Rumex* that come together at the maturation of the pollen mother cells (fig. 7) and then separate, the two smaller going to one pole and the single large chromosome to the (fig. 7) and also in *Melandrium*. He also found in *Vallisneria* an unpaired chromosome (X) in the male. In the latter case, half the pollen grains have one X (and eight autosomes) and half no X (and eight autosomes).

Miss Blackburn also reported an un-

equal pair of chromosomes in the male of *Melandrium*, (fig. 7) and has also a further fact essential to complete the chain of evidence, namely, that in the female there is an equal pair of corresponding chromosomes. She thought it probable that the two chromosomes in the female correspond to the smaller (Y?) chromosome of the male but the more recent observations of Meurman (fig. 9) indicate that the two chromosomes in the female correspond more nearly to the size of the larger (X) chromosome of the male.

Blackburn and Harrison reported that an unequal pair of chromosomes is present in the male of the poplar (*Populus tremula*) and in the male of a willow (*Salix viminalis*).

Hirata found in one race of hemp (*Cannabis sativa*) an unequal pair of

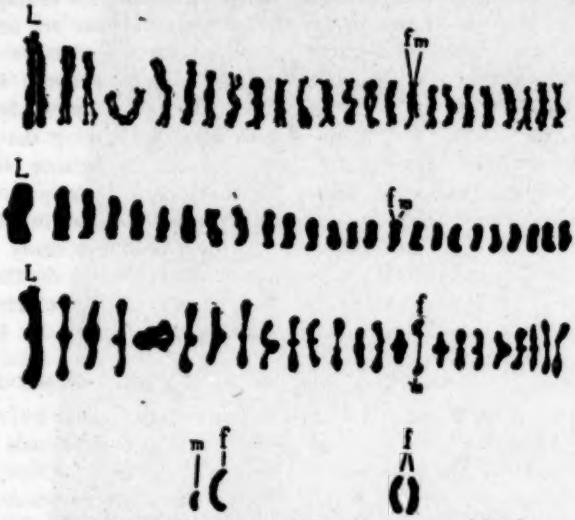

FIG. 8. PAIRED CHROMOSOMES (GEMINI) OF ELODEA (MALE)

The two upper lines include the XY pair (*f* and *m*) in conjugation; in the third line they are in process of separation. In the fourth (lowest) line the difference in size between X and Y (here *f* and *m*) in the male is shown to the left, and the two X's (of the same size) are shown to the right. (After Santos)

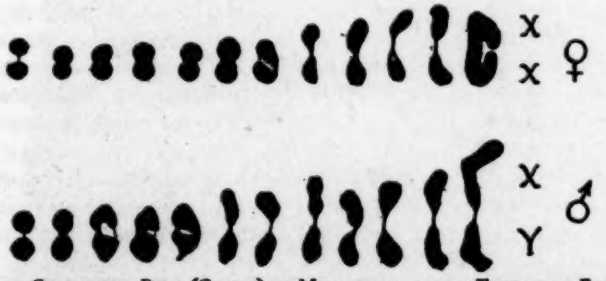

FIG. 9. TWELVE CHROMOSOME PAIRS (GEMINI) OF MELANDRIUM ALBUM; THOSE FROM FEMALE IN THE UPPER LINE WITH X-X PAIR; THOSE FROM MALE IN LOWER LINE WITH X-Y PAIR
(After Meurman)

chromosomes, although McPhee had failed to discover such a difference in the variety of hemp studied by him. These results with hemp are interesting since it has been shown that environmental conditions have an effect on the development of male and female flowers on the same plant, at least in certain races. Yampolsky reports that in *Mucuralis* there is not an unequal pair of chromosomes in the male.

The latest report on the subject by Meurman adds a number of other cases to this list for the male, and confirms several of the earlier results. In three species of poplar he reports an unequal pair in the male. He finds the same relation in *Valeriana* and probably in *Urtica* and in two varieties of *Melandrium* (fig. 9). A tripartite chromosome is present in the male of two species of *Rumex*. In one species of *Dioscorea* (*D. sinuata*) there is probably an unpaired chromosome in the male, and two classes of pollen with 17 and 18 chromosomes were observed in one case in sister "plates." In another species no inequality in the pair could be observed. In six other dioecious plants no inequality in any of the chromosome pairs could be detected.

These observations go far towards establishing the view that there exists in some dioecious plants a chromosome mechanism that determines sex. The male is digametic in all cases so far described as earlier experiments by Correns and by Shull had made probable. The mechanism is the same in kind as the XX–XY type in many insects. It should be pointed out with all possible emphasis that this correspondence in mechanism does not necessarily mean that the two processes are comparable as to the genes involved. Only if sex is generalized and supposed to be in all cases the result of the same specific sex-genes that are common to all organisms could there be any grounds for such an assumption. There is as yet no evidence of specific genes that have to do with sex determination alone and least of all any grounds for such an assumption when for example a flowering plant and an insect are compared. The evidence seems rather to mean that a certain balance between sets of genes, possibly a very large number, inclines the individual to develop the male sex-cells, while another balance tips the scale another way. It is quite possible that there is not one way in which the scale may be tipped but many ways. If so, sex-determination in the flowering plants may be due to different sets of genes from those that determine sex in animals.

SEX IN HAPLOIDS

The demonstration by Allen in 1919, that the cells of the female haploid gametophyte of the liverwort, *Sphaerocarpus*, have a large X-chromosome and that the cells of the male haploid gametophyte have a corresponding small Y-chromosome, gives a reasonable explanation of the differences shown by their prothallia (gametophytes). Similarly the experimental demonstration by the Marchals, by Wettstein and others that from each spore-mother-cell of dioecious mosses arise two spores that develop into female protonemata (gametophytes), and two other spores that develop into male protonemata (gametophytes), falls into line with Allen's results on the allied liverworts. It is customary to speak of the two kinds of gametophytes as female and male respectively since one produces eggs the other sperm cells (antherozoids). The succeeding generation, the sporophyte (zygote) arising from the fertilization of the egg by the sperm, is sometimes said to be sexless or asexual. It has however one X- and one Y-chromosome.

Some unnecessary confusion has arisen between the terminology used for the moss and liverwort and that employed for dioecious flowering plants in which the terms female and male apply to the sporophyte (diploid) generation and not to the egg cell (which is a part of the haploid generation within the embryo sac) and to the pollen grain (which is also a part of the haploid generation). It may seem at first sight, that male and female are used in these two groups in a different sense. There is no real contradiction, however, except a verbal one arising from phylogenetic implications. If the two cases in question are stated in terms of genes, the imagined difficulties disappear. In the liverworts, for instance, the balance of genes in the haploid gametophyte, containing the large X-chromosome, leads to the production of egg-cells and the balance of genes in the haploid gametophyte containing the small Y-chromosome leads to the production of sperm-cells. The egg-bearer is here called female, the sperm-bearer is called male. In the diploid generation of those flowering plants that are dioecious, where a differential pair of chromosomes is present in the male, the balance of the genes in the diploid generation between the autosomes and two X's gives a female (an individual that produces eggs), and the balance of the genes in the diploid generation between the autosomes and the XY pair gives a male (an individual that produces sperm cells). Both in the liverwort and in the flowering plant the situation turns on a balance between sets of genes. It may be that the same sets of genes are not involved in both cases, or that some of them are the same, others are different. The essential point is that in both cases, differences in balance lead to two kinds of individuals which are called males and females since they produce eggs and sperm cells respectively.

In criticism of these statements it may possibly be said that the facts have only been restated and not explained. This is quite true. All that has been attempted is to point out that the facts may be restated in such a way that there is no apparent contradiction involved in the two cases. We may look forward perhaps to the time when the number and nature of the genes involved in cases where a difference in balance produces two kinds of individuals, will be determined. Meanwhile there is nothing in the situation that need cause anxiety, and certainly nothing that can be used as a refutation of recent advances in an understanding of sex determination.

The haploid condition in animals is characteristic of the gametes. There are no cases of alternating haploid and diploid generations as in plants. But there are two or three types at least in which one sex is diploid and the other haploid. In the Hymenoptera and a few other insects the female is diploid and the male haploid, at least in the early stages of development. In Rotifera the females are diploid and the males are haploid. There is no evidence in either group of sex-chromosomes as such. At present no explanation resting on experimental evidence can be offered to explain these relations. Until such evidence is forthcoming the possible theoretical interpretations that have been suggested are not illuminating.

In *Drosophila* on the other hand where a known sex mechanism is at hand, and where there is experimental evidence bearing on the problem of balance of the genes involved in sex-determination, there is a recent observation by Bridges that is significant. Two mosaic individuals were found which, from genetic evidence, seemed probably to be composites, in part haploid and in part diploid. In one case the haploid region includes the loca-

tion of a secondary sex-organ, the sex-comb (present in the normal male, absent in the female). In the mosaic the sex-comb is absent in the region that is haploid. In other words the haploid group of chromosomes consisting of three autosomes and one X gives, as anticipated, the same kind of result as six autosomes and two X's. The balance is the same in each although the haploid region of the mosaic has only one X, as has the normal male; but in the male this is offset by six autosomes.

The converse case is reported by Wettstein who produced by artificial means gametophyte moss plants that were diploid. If these arise from a haploid female gametophyte cell they are female, and if from a haploid male gametophyte cell they are male. In both cases the balance remains as before. It is apparent that sex determination is not in these cases regulated by the number of the chromosomes but by the relation of contrasted sets of genes or chromosomes to one another.

SEX AND ITS DEFINITION IN LOWER PLANTS

The question of sex terminology appears in its most acute form in the results of recent work on certain groups of gilled fungi or toadstools, Basidiomycetes. In this group, according to a recent statement by Hanna "The problem of sex has occupied the attention of mycologists for more than a hundred years." The discoveries of Miss M. Bensaude (1918), of Kniep (1919–23), of Miss Mounce (1921–22), Buller (1924) and Hanna (1925) have brought to light an extraordinarily interesting situation. In order to simplify the description of this work, the recent paper of Hanna is here followed closely. By means of a new and refined technique, single spores from the gills of the toadstool can be isolated. From each spore a single mycelium of hyphae can be grown in dung-agar cultures. Each such monosporous mycelium can then be tested by bringing it in contact with the others one by one. Certain of these combinations will unite and form a secondary mycelium on which "clamp connections" develop, indicating that the two mycelia are of "opposite sexes." Later, fruiting bodies or toadstools develop from such mycelia. On the other hand, other combinations when made, do

		AB			ab				Ab		aB
		51	52	54	55	57	58	59	50	56	53
AB	51	−	−	−	+	+	+	+	−	−	−
	52	−	−	−	+	+	+	+	−	−	−
	54	−	−	−	+	+	+	+	−	−	−
ab	55	+	+	+	−	−	−	−	−	−	−
	57	+	+	+	−	−	−	−	−	−	−
	58	+	+	+	−	−	−	−	−	−	−
	59	+	+	+	−	−	−	−	−	−	−
Ab	50	−	−	−	−	−	−	−	−	−	+
	56	−	−	−	−	−	−	−	−	−	+
aB	53	−	−	−	−	−	−	−	+	+	−

FIG. 10. RECORD OF UNION (+) OR FAILURE (−) BETWEEN MONOSPOROUS MYCELIA OF COPRINUS LAGOPUS OF SAME PARENTAGE

The mycelia are here classified into four kinds, AB, ab, Ab, aB, according to their behaviour with one another. (After Hanna.)

not form secondary mycelia with clamp connections, and, as a rule, do not produce fruit bodies. The union is interpreted to mean that the mycelia in question are of opposite sex.

Now, when monosporous mycelia from the same strain, (i.e., from plants living in the same locality) are tested, the results are like those in Fig. 10. Here, the presence of clamp connections, formed after the union of two monosporous mycelia, is indicated by the + sign. Failure in this respect is indicated by the −

sign. In the table the mycelia fall into four groups (those belonging to the same group have been brought together in the table). The result is interpreted as meaning that the spores of a single fruit body of the species studied namely *Coprinus lagopus*, belong to four sexual groups.

These four groups as Kniep first showed, can be accounted for on the assumption of two pairs of Mendelian factors that may be designated Aa and Bb. If these factors are segregated, at the time when the sporous mycelia lie singly in the protoplasm. After union of two mycelia, the nuclei in the derived (secondary) mycelium are in pairs. It is reasonable to assume that one member of each pair has come from one mycelium, the other one from the other mycelium. At the time when the four spores are about to develop, reduction is supposed to take place, so that each spore comes to contain a reduced nucleus. Each spore gives rise to a new reduced mycelium. Such a picture

		A^4B^4			a^4b^4			A^4b^4			a^4B^4		
		4	7	8	5	2	6	10	11	1	3	9
A^2B^2	25	+	+	+	+	+	+	+	+	+	+	+
	26	+	+	+	+	+	+	+	+	+	+	+
	27	+	+	+	+	+	+	+	+	+	+	+
	28	+	+	+	+	+	+	+	+	+	+	+
a^2b^2	20	+	+	+	+	+	+	+	+	+	+	+
	23	+	+	+	+	+	+	+	+	+	+	+
	24	+	+	+	+	+	+	+	+	+	+	+
a^2B^2	21	+	+	+	+	+	+	+	+	+	+	+
	29	+	+	+	+	+	+	+	+	+	+	+
	30	+	+	+	+	+	+	+	+	+	+	+
A^2b^2	16	+	+	+	+	+	+	+	+	+	+	+

FIG. 11. RECORDS OF UNIONS BETWEEN UNISPOROUS MYCELIA OF COPRINUS LAGOPUS FROM DIFFERENT STRAINS, $A^1\,a^1\,B^4\,b^4$ AND $A^3\,a^3\,B^2\,b^2$.
(After Hanna)

spores are formed on each basidium, there will be present on each toadstool four kinds of spores, AB, ab, Ab, aB, each of which gives rise to a mycelium of the same genetic composition. As shown in figure 10, only those mycelia differing in both factors unite and form clamp connections. This means that there are four sexes, and only those with different sex factors can combine.

There is also a cytological background that accords excellently with these genetic assumptions. The nuclei in the monoaccords with the reduction process in higher plants and animals and serves to bring these moulds into line with the genetic results that take place when the chromosomes are reduced from diploid to haploid gametes. It is true that, as yet, it has not been shown in *Coprinus* and related species that we are dealing with a diploid-haploid relation, but it seems not improbable that this is the correct interpretation of the facts as far as known. If so, the sorting out of the genetic factors in these toadstools is the

same in principle as that shown by other plants and animals.

The preceding relations hold for strains occurring in any one locality. If strains from different localities are tested, an extraordinary result is found. All the monosporous mycelia of one strain unite (i.e., give mycelia with clamp connections, etc.) with all the monosporous mycelia of the other strains. In figure 11 the pairing of eleven monosporous mycelia from a fruit body from one locality (Edmonton, Canada) are shown to have united with eleven monosporous mycelia from another locality (Winnipeg). The same results were obtained whenever strains from different localities were paired. The combinations carried out by Hanna gave twenty sexes for *Coprinus* and no doubt the number could be greatly increased by extending the combinations to other localities.

Not only was cross-hybridizing carried out, but the factorial hypothesis was further tested by experiments on the crossed strains themselves. If the factors from the different strains are treated as allelomorphic pairs, and the factors in one strain are designated by Aa and Bb, and those in another strain by A^2a^2 and B^2b^2; there will be sixteen possible hybrids formed by the union of the mycelia from these two varieties, and each mycelium of such hybrid origin will behave in a manner similar to that shown by mycelia from a single source, in that two given mycelia form clamp connections only in case they carry no factors in common.

Here we have the phenomenon of sex exhibited on a grand scale if we interpret the factors involved as sex factors in the conventional sense. There is no objection to using the word in this way if it seems advantageous to define sex on such a basis. Personally, I think it is simpler to interpret the results in the same way as East has interpreted the results of his tobacco investigations, and call the factors involved self-sterility factors (see below). The explanation is the same in principle, whatever language one prefers to use in describing them.

FIG. 12. SWARMING OF MALE GAMETES AROUND "FEMALE" GAMETE (TO LEFT). UNION OF A "MALE" GAMETE AND A "FEMALE" GAMETE (TO RIGHT)
(After Hartmann)

Under the title of Research on Relative Sexuality, Hartmann has recently described results that he obtained with the marine alga, *Ectocarpus siliculosus*. The motile swarm-spores set free from the plants are externally alike, but according to their subsequent behavior they fall into two classes "females" and "males." The former quickly settle down, while the latter continue to swarm for some time and surround the female individual (fig. 12). One of the male swarm-spores finally fuses with the resting female swarm-spore. Hartmann isolated individual parent plants

and when the swarm spores were set free tested these *en masse* against each other. A typical result is given in figure 13 (to the left) where union is indicated by the + sign and failure to unite by the − sign. Each kind is tested against each of the other kinds. In most cases the swarm-spores from a given individual behave constantly either as males or as females with the other types, but in a few instances swarm-spores that acted as females in some combinations acted as males in other combinations. Thus No. 4 (see fig. 13, to left) and No. 13 give results inconsistent with their reaction

	3♂	4♀	5♀	7♀	11♂	13♀	14♀
3♂	−	+	+	+	−	+	+
4♀	+	−	−	−	+	+	−
5♀	+	−	−	−	+	−	−
7♀	+	−	−	−	−	+	−
11♂	−	+	+	−	−	+	−
13♀	+	+	−	+	+	−	+
14♀	+	−	−	−	−	+	−

	31♀	32♀	33♂	35♂	38♂	40♂
31♀	−	−	+	+	+	+
32♀	−	−	+	+	+	+
33♂	+	+	−	+	−	−
35♂	+	+	+	−	+	−
38♂	+	+	−	+	−	−
40♂	+	+	−	−	−	−

FIG. 13. RECORD OF UNION (+) OR FAILURE (−) TO UNITE BETWEEN THE GAMETES FROM DIFFERENT PLANTS (ECTOCARPUS)
(After Hartmann)

in other combinations. Another exception is found in the reactions between No. 35 and No. 38 (see fig. 13, to right), both of which are designated as males from their general behaviour, yet react to each other as male and female. Hartmann speaks of certain individuals as strong males, others as weak males, certain individuals as strong females and others as weak females according to the numbers of "clusters" that they give in different combinations, and concludes that weak females may function as males when opposed to strong females, and that weak males may function as females when opposed to strong males. To what extent these relations may be affected by age-factors (settling down, for example), or by environmental factors is not entirely clear, although Hartmann's statement that the relations hold from day to day as the swarm-spores are tested seems to exclude such explanations. Unfortunately the material is not suited to a genetic analysis of the factors involved. Whether the quicker settling down of gametes from a certain individual is a sufficient index of their "sex" and if so, how this is changed when a weak female acts as a male, etc., is not apparent. Nevertheless the failure of gametes from the same plant to copulate appears to put the phenomenon in the same category as self-sterility present in other groups. Whether self-sterility and its correlative cross-fertility is to be taken as a criterion of sex is perhaps largely a matter of choice or of definition at present. Personally it seems to me to confuse rather than clear up the problems involved to use the word sex in this connection where the phenomenon is rather one of union of gametes or their failure to unite—due possibly to self-sterility factors—than one of sex as commonly understood.

The question may be seriously asked whether it may not be simpler and less

likely to lead to confusion to call the factors involved in the union of the mycelia of *Coprinus* and of the swarm-spores of *Ectocarpus*, self-sterility factors rather than sex-factors. The recent brilliant results of East in his studies on self-sterility in tobacco have for the first time put the oft-studied problem of cross- and self-fertility in flowering plants on a well tested genetic basis. These phenomena in the flowering plants have many resemblances to the union of the gametes in *Coprinus* and *Ectocarpus* and while the *modus operandi* of the process may not be identical in all cases there is much to suggest that the genetic and physiological backgrounds may be essentially alike.

In the brief paper of East and Mangelsdorf is given a summary of work extending over several years dealing with the inheritance of self-sterility in crosses between two species of tobacco, viz. *Nicotiana alata* and *N. forgetiana*. Only the most general conclusions can be given here. By special manipulation several selfed, homozygous strains of self-sterile individuals were carried through twelve generations to obtain suitable material for testing the problem. As an example the results of one type of the resulting families may be given. Three kinds of individuals a, b and c were found. Each individual of any one of these kinds is sterile with any other individual of the same class and fertile with each individual of the other two kinds; but the progeny resulting from reciprocal crosses is different. Thus, a ♀ by c ♂ gives b and c individuals only, while c ♀ by a ♂ gives only a and b individuals. Two classes always appear in equal numbers, but the class of the mother is never represented in the offspring. The explanation is as follows. If three allelomorphic genes are present in such a family S_1 S_2 S_3 and if class a = S_1 S_3; class b S_1 S_2; class c S_2 S_3 and if the pistil of a plant affords the stimulus for the growth of the pollen which bears sterility factors other than its own, the results find a consistent explanation. For instance, plant c (S_2 S_3) affords a sufficient stimulus only to pollen carrying factors other than S_2 S_3. Only pollen bearing the factor S_1 can penetrate the style and fertilize the eggs. The progeny will be S_1 S_2 (class b) and S_1 S_3 (class a) in equal numbers. Reciprocally, a ♀ (S_1 S_2) by c ♂ (S_2 S_3) permits the S_2 pollen alone to penetrate to the eggs giving S_1 S_2 (b) and S_2 S_3 (c). This result which is typical of all the others, explains why the female combination is absent in the progeny, why the progeny of reciprocal crosses is different and why the progeny-counts of two classes other than the female are equal regardless of which of the other two classes serves as the male parent.

There are several ways of testing the validity of this hypothesis. The tests have been made and the hypothesis confirmed. This convincing analysis, the result of carefully planned genetic experiments, is a contribution of the first rank to a problem that has baffled students of fertilization for seventy-five years and more. The solution is not only a keen genetic analysis of the case but gives an insight into the physiological reactions between the haploid pollen tube and the diploid tissue of the female. It has been shown by direct observation that the rate of growth of the pollen tube in the tissue of the female is consistent with the view that a differential rate of growth is actually present. The nature of the relation is not known at present but may reasonably be assumed to be chemical in nature. It is possible that the same or a similar chemical reaction with its genetic basis may account for the

self-sterility observed in the union of genetically unlike mycelia of lower forms. If this can be established the genetic problem has to deal primarily with self-sterility factors that are probably Mendelian genes. It may seem of doubtful value to identify these factors with sex factors which conventionally at least apply rather to somatic differences in dioecious types or to those with separate sexes. It is true that amongst these differences are those concerned with producing eggs and sperm whose main function is to unite with each other, but, as generally understood, these functions are less conspicuous than those appertaining to the bodily constitution of male and female individuals.

GENES IN THE Y-CHROMOSOME

Earlier work on the sex-cells of those insects that have an unequal pair of sex-chromosomes in the male had shown that the smaller member (Y) of the pair is confined to the male line. In different species all degrees of inequality between X and Y were soon discovered, and in a few cases no Y at all was found, leaving the X as an unpaired chromosome in the male. Since in the last case it was obvious that a Y-chromosome is unnecessary for the production of a normal male, the variation in size of the Y in different species gave the impression that the Y-chromosome had less significance in sex determination than the X-chromosome, and might even be lost without any change in the mechanism. The female would thus be due to the presence of two X's and the male to the presence of one X-chromosome.

This implication resting on cytological findings seemed to be confirmed by the discovery that the Y-chromosome of *Drosophila melanogaster* does not carry a set of genes comparable to those found in the other chromosomes, or more accurately stated, the inheritance of characters whose genes are carried by the X-chromosomes may be treated as though the Y-chromosome carries no genes that are dominant to them; in other words, that the Y-chromosome may generally be ignored or treated as though it were "empty." Taken literally the last statement seemed absurd and has furnished some of the critics of the chromosome mechanism with material for ridicule. These critics have generally overlooked the fact that the above statements about the Y-chromosome are no more than a conclusion from genetic evidence which they would scarcely dispute. They overlooked also the fact that the workers in *Drosophila* have been careful to state, more than once, that their results do not show the Y-chromosome to be empty except in the sense that it contains no genes that have as yet been found to behave as dominants to recessive genes of the X-chromosome. Moreover, it is sometimes forgotten that a male *Drosophila* without a Y-chromosome is sterile although in all other respects his characters are normal. It has further been shown that the presence of a Y or even two Y's in the female (which is occasionally brought about by its transfer from the male line) does not affect the female characters in any visible degree. Its presence causes irregularities in the distribution of the sex-chromosome at the maturation division, in the same way as does an unpaired chromosome of any other pair, but this concerns rather the mechanism of reduction, and does not relate to the genic composition of the Y-chromosome itself. Until evidence is brought forward that the Y-chromosome of *D. melanogaster* carries genes that must be reckoned with in the study of inheritance, the facts enumerated above may stand.

Some recent discoveries, furnishing genetic evidence that the Y-chromosome in other animals carries genes comparable to the genes in other chromosomes and that the genes cross over with those in the X, have been hailed with delight by the opponents of the chromosome theory as evidence that the conclusions concerning the Y-chromosome in *Drosophila* are in some way compromised. There is, however, a probable solution that involves a familiar cytological conclusion, namely, that the sex-chromosomes may be a part of, or have become attached to, a pair of autosomes. This means no more than that one part only of the "sex-chromosomes" has the function of an X-or Y-chromosome, which means again that the Y-part is different from the X-part, and that no crossing-over takes place between these parts. The following diagram (fig. 14) will serve to illustrate how this mechanism gives the same kind of result, so far as sex is concerned, as does the occurrence of independent sex-chromosomes. There is involved, however, another set of problems relating to sex-linked inheritance.

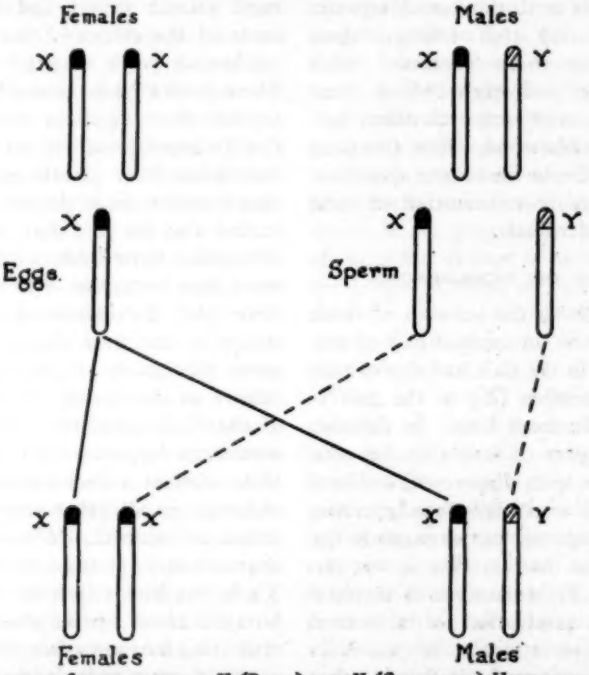

FIG. 14. DIAGRAM OF SEX-CHROMOSOMES, X (BLACK) AND Y (CROSS-LINED) UNITED TO AUTOSOMES

If there is no crossing over between the X- and the Q-component in the male, the Y-chromosome remains in the male line.

If no crossing-over takes place between X- and Y-components, but may take place between the autosomal parts of this pair, the inheritance of characters whose genes are carried in the autosomal parts will be expected to show partial linkage to sex and to the characters whose genes lie in the X-component. It is not necessary to point out here the details of this sort of inheritance, but it may be stated

that it will be consistent with the facts so far reported for cases where the "Y" is said to carry genes that interchange with those of the "X." A few facts recently obtained may be cited.

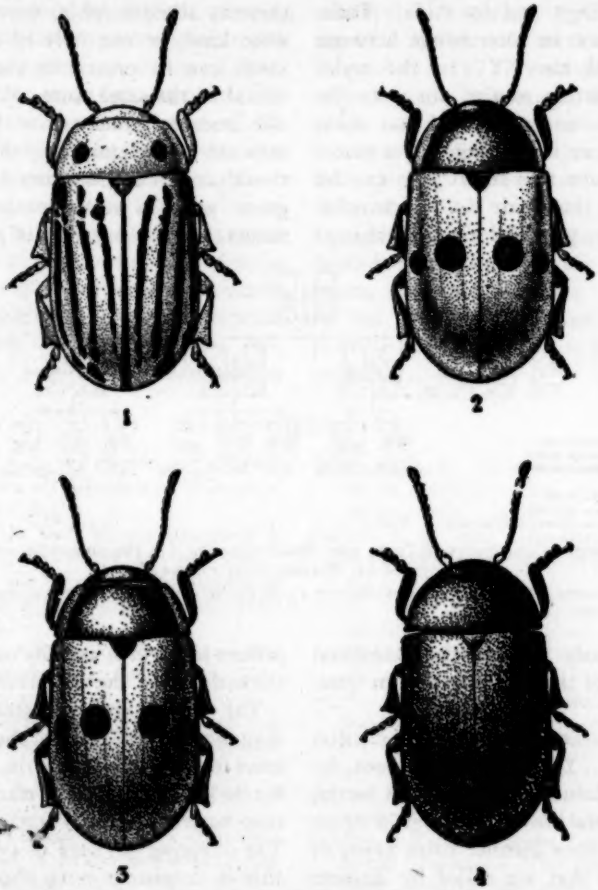

FIG. 15. FOUR TYPES OF THE BEETLE, PHYTODECTA VARIABILIS, NAMELY, 1, DE LINEAS; 2, AMARILLO; 3, ROJO; 4, NEGRO
(After Zulueta)

In the aquarium fish, *Lebistes reticulatus*, the females of different races are closely similar in coloration while the males are differently marked. It was shown first by Schmidt (1920) and later confirmed by Winge, that when the male of one race is bred to a female of another race the sons are colored like the father. If these hybrids are inbred, the sons are again like the father, i.e., they have not inherited any color through the mother. The same relation appears in later generations and in all combinations tested. A similar type of inheritance was independently discovered by Aida in another

fish, *Aplocheilus*, inhabiting the paddy fields of Japan. The results are explicable on the view that the genes for the different kinds of colors are carried both by the X- and by the Y-chromosome.

A further fact of importance was reported by Winge and by Aida. There may take place an interchange between the "X" and the "Y" in the male, or at least certain results can only be explained on the assumption that occasionally such an interchange takes place. As stated above this result also can be brought into line with the sex-chromosome formula, provided the interchange takes place only between the autosomal components of the chromosomes in question.

A remarkable case of transmission through the "Y" has recently been described by Zulueta for a Spanish beetle, *Phytodecta variabilis*. As shown in figure 15 there are four distinct color types of these beetles that are called by Zulueta (1) de líneas, or striped, (2) amarillo, or yellow, (3) rojo, or red, and (4) negro, or black. Crossing experiments with these types show that any one of them behaves towards any other one as an allelomorph. In other words, the genetic results can be treated as a case of multiple allelomorphism.

The experiments show that type de líneas (L) is recessive to any of the others, that amarillo (A) is in turn recessive to the other two, that rojo (R) is recessive to negro (N). The order of dominance is L<A<R<N. Treating these as allelomorphic, only two of the same kind, or one only of each of two kinds can be present in the same individual at the same time. A further fact also emerges, namely, that the genetic results can be explained only on the assumption that the chromosomes that carry these genes are the sex-chromosomes. This means that any one of the genes may be present in the X's, and any one in the Y of the male line. The sex formula is XX–XY.

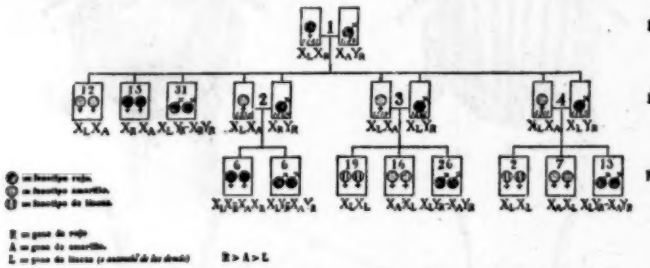

FIG. 16. PEDIGREE OF A CROSS BETWEEN TYPES, ROJO, FEMALE (SEE FIG. 15), HETEROZYGOUS FOR DE LÍNEAS AND TYPE ROJO, MALE, HETEROZYGOUS FOR AMARILLO

The Y-chromosome is here represented as carrying a gene for rojo, and the X-chromosome as carrying the allelomorphic gene. (After Zulueta.)

The experiment illustrated in the diagram (fig. 16) gives the results of a cross in which a female rojo, heterozygous for de líneas ($X_L X_R$) is mated to a male rojo heterozygous for amarillo ($X_A Y_R$). The offspring (F_1) are of two kinds, and this is consistent with the formula employed. Certain of the F_1's were mated to each other to give an F_2 generation. Here three types appear which again are expected. Other matings give the same kinds of results, all of which can be interpreted as above, on the assumption that the Y-chromosome may carry any one of the four genes.

If these genes are in the sex-components which, *ex hypothesi*, do not interchange, the question arises as to how the same kinds of allelomorphs may be present in the X- as well as in the Y-component. One answer would be that they have arisen from the same kind of original gene as independent mutations, sometimes in the X-component, sometimes in the Y-component. There are, in fact, some curious facts relating to the distribution of the males in different districts,—facts that are perhaps consistent with the above assumption of independent mutation in X and Y. In some districts certain mutant types of males are absent while in other districts these types are abundant. This is consistent with the assumption of independent mutation in the two chromosomes, but another explanation will do as well. Suppose, for instance, that the genes for the four color markings are not present in the X- and Y-components but in the autosomal components and that they are allelomorphs. The results will then be explicable on the assumption that there is either no crossing-over in the male or that it is so infrequent as not to have arisen in Zulueta's experiments. If, however, it should take place on rare occasions in the male between the autosomal components, the facts relating to the distribution of the different kinds of males may be accounted for. Hence on either view, that of independent mutation in the sex-chromosomes, or that of rare crossing-over in the male in the autosomal component, the facts as far as known can be explained.

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THE ANTIQUITY AND DISPERSAL OF VASCULAR PLANTS

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Gray Herbarium, Harvard University

AGE AND AREA

A DECADE ago (**79**, p. 325), after compiling and studying statistics covering the endemic vascular plants of Ceylon, Dr. J. C. Willis put forward his "law" of Age and Area; and a year later he had so far progressed in his studies as to state that "The law which appears to me to govern the distribution of species may be thus tentatively expressed: 'the area occupied by any given species (taken in groups of twenty or so) at any given time in any given country in which there occur no well-marked barriers depends upon the age of that species in that country'" (**81**, p. 438). Extending his statistical studies to the Angiosperms and sometimes to the Pteridophytes of New Zealand, Brazil and other areas, including oceanic islands and the British Isles, Willis continued to amass a body of summaries and generalizations and to enunciate corollaries at a rate quite dazzling to others.

The original proposition, reduced to its simplest terms, might well be stated: given a static world the longer a plant (or animal) lives the more opportunity it will have to spread; consequently, the older a species the wider its range. But at once Willis was challenged by close students of various floras, who pointed out that, although the primary "law" (which Willis later more modestly referred to as his "hypothesis" and subsequently (**91**, p. 246) as "simply a corollary") is axiomatic, the world, as a matter of fact, has been anything but static and that the present ranges of plants and animals are due to such a complex of historic and edaphic factors that their ages cannot safely be deduced by studying simply the extent of their present distribution. Many other objections were brought forward by students of floras or faunas, chiefly of England, India, South Africa and North America; while by the mutationists Willis was vigorously applauded.

So long as the discussions were confined to a few journals, and principally to *Annals of Botany*, they were seen by only a limited number of students, but in 1922 Dr. Willis drew together in modified form his chief arguments, and had them supplemented by chapters contributed by some of his supporters, in a handy volume (**91**) now familiar or readily accessible to all. During the discussions which had followed the publication by Willis of his many deductions his definition of Age and Area greatly altered, a change clearly brought out in the statement by Gleason:

> Originally it was, in essence at least, "The area of a species depends on its age;" but now, since one exception after another has been added, it reads:
>
> "The area occupied at any given time, in any given country, by any group of allied species at least ten in number, depends chiefly, so long as conditions remain reasonably constant, upon the ages of the species of that group in that country, but may be enormously modified by the presence of barriers such

as seas, rivers, mountains, changes of climate from one region to the next, or other ecological boundaries, and the like, also by the action of man, and by other causes."

One can count in this expression of the theorem no less than nine distinct exceptions definitely stated, relating conditions under which the age-and-area principle may not hold. Then, to guard against other criticisms which may arise in the future and which Willis was unable to foresee, he has added the blanket exception "other causes." Lastly, to make his theorem still more nearly impregnable, he has forbidden us to argue against it by citing individual exceptions. In other words, the area of a species depends on its age when it does depend on it, and cases in which it does not must not be mentioned (39, p. 342).

Very frankly, I had supposed that Willis, by piling up so many exceptions in his definition and by shifting at will the magic number of test-cases which one must use, sometimes twenty, sometimes fifteen, sometimes ten, had proved Age and Area a dead issue; and I thought that such students as Bateson (4), Berry (5, 7), Calvert (13), Regan (62), Ridley (65, 66), Schonland (69), Seward (70), and Sinnott (71, 72, 73), had seen it officially buried. But the facts, that in 1923 I was urged to take part in a symposium upon the subject and that I am now again invited to act as medical examiner and coroner, indicate that to those who are not specially in touch with the problems of classification and distribution the hypothesis seems still alive and to make a strong appeal. This is quite natural, for we all take an interest in the larger generalizations in biology and Age and Area is a large generalization. I must, however, make it quite clear that, in a limited discussion I necessarily confine myself chiefly to the few aspects of the question with which I am most familiar and, since Willis, himself, enumerates and discusses many of the objections which have been raised and since they have been clearly discussed by the scores of careful thinkers referred to in my bibliography, I must refrain from entering at this time into many of these matters.

In some instances I do not understand what Willis means, but I take comfort in the fact that I am not alone. He repeatedly complains that others do not have "a proper understanding of Age and Area, and of the provisos with which it is hedged around" (91, p. 84); Lloyd Praeger, than whom there are few if any keener students of plant geography in Great Britain and Ireland, says: "to be candid, I find it difficult to follow and doubt if I understand it fully. . . . . Recently . . . . I had the advantage of discussing the theory with its author; but . . . . I failed to obtain a clearer understanding. Like the Persian philosopher, I came out by the same door as in I went" (61, p. 122). Bateson characterized the book, *Age and Area*, as "very difficult reading" (4, p. 43) and Berry speaks of Willis's ideas as "embalmed in a very complicated style" (7, p. 547).

The introductory chapters are on the whole really fine and, as Bateson said, clearly demonstrate that Willis actually knows that the world is *not* static. Praeger, too, finds these chapters sane and sound, forming an excellent modern introduction to a general study of phytogeography. But one must wonder at many of the illustrations used and some of the statements of fact. Willis claims not to believe in *adaptations* and in his arguments that they are rarely found in fruits he is very catholic, for he includes among the "genera with little or no mechanism for dispersal" (91, p. 21) the tick trefoils (*Desmodium* or *Meibomia*), the fruits of which are unwillingly transported by every passing animal. And, in arguing that the largest families of plants (excepting *Compositae* and *Orchidaceae*) "are not remarkable for the posses-

sion of extra good methods of dispersal" (91, p. 21), he enumerates among the examples Milkweeds, *Asclepiadaceae* (which are characterized by having thin and flat seeds with a long coma), the Heaths, *Ericaceae* (many with berries or with fine seeds suggesting those of orchids), Grasses (which he elsewhere admits "to some degree suited to wind dispersal"), the *Rosaceae* (many with fleshy fruits, fine seeds or plumose or bristly fruits), the *Coniferae* (mostly with winged seeds) and the Figworts, *Scrophulariaceae* (chiefly with fine or thin seeds). If these and many others enumerated by Willis appeal to him as lacking adaptations for dispersal, it would seem that he sees adaptations only in bizarre modifications.

RATE OF MIGRATION OF PLANTS

In these introductory chapters Willis makes much of the well known slow rate of migration of most plants and rightly contends, what any ecologist or other student of vegetation in the mass will approve, that in studying distribution whole associations must be taken into account, since the different species move together and are so closely interrelated that an outsider would find it difficult to gain a foothold within the association. As plants with power of specially rapid spread he cites (following Ridley) those with light powder-like seeds or spores as most rapidly spread, those with plumed seeds (dandelion, etc.) next and those with winged seeds (ash, maple, pine, etc.) "the slowest" of those with special mechanisms for dispersal; while plants with seeds like those of bur-reeds (*Sparganium*), *Iris*, *Corydalis*, peas (*Lathyrus*, etc.), touch-me-not (*Impatiens*), violets (*Viola*) and buckbean (*Menyanthes*), solid, rounded and heavy, without plumes or wings, would presumably be classed as completely handicapped. He cites the Dipterocarps, "tall trees with . . . . fruit, upon which . . . . grow large wings," as fairly rapid travelers, but even in these "a little calculation will show that in the most favorable circumstances conceivable, with the ground clear of other vegetation, it would take about 60,000 years to migrate 100 miles. *Dipterocarpus grandiflorus* . . . . ranges from the Malay Peninsula to the Philippines, and Ridley estimates that at least 1½ million years would be needed to traverse this distance" (given continuous land, of course). The distance from the Malay Peninsula to the Philippines is 1000 miles. If specially favored plants with an absolutely clear field would require 1½ million years to cover this distance, what shall we say of the vast Canadian and Hudsonian flora of cool-temperate North America?

This great group of plants of all habitats (coniferous or mixed forest, bog, cliff, rock-barren, sand-hill, stream, lake, meadow, etc.) must, we agree with Willis, be considered as moving *in toto*, not as individual species. Yet this great body of plants, occupying about one-fourth of the area of North America, could not invade the Canadian and Hudsonian country from the South until the receding from it of the last Pleistocene ice. In other words, the plants had before them the absolutely clear field required for the hypothetical migration of the wind-dispersed Dipterocarp, which, according to Willis, would require 1½ million years to cover 1000 miles. Very conservatively, geologists set 25,000 years ago as the time when the southern edge of the Wisconsin ice began to recede and, of course, a later date when it left the North, very much later since "The time occupied by the recession from

Hartford [Connecticut] to St. Johnsbury [Vermont, a distance of 190 miles] was about 4100 years" (2, p. 74). Yet, as clearly shown in the excellent little maps published by Hough (48), the trees of the Canadian forest have occupied an area varying in length (east to west) from 3800 (practically 4000) miles (White Spruce, *Picea canadensis*—map 1, Balsam Poplar, *Populus balsamifera*, Canoe Birch, *Betula papyrifera*, etc.) to a general minimum of 2000 miles (Red Pine, *Pinus*

MAP 1. RANGE OF WHITE SPRUCE, PICEA CANADENSIS, AFTER HOUGH (48)

resinosa, White Cedar, *Thuja occidentalis*, American Mountain Ash, *Sorbus americana*, Mountain Maple, *Acer spicatum*, etc.). North and south, within the area of the latest glaciation, the belt is 500 to 1200 miles across. And, occupying the same extremely youthful area with the trees, which have winged fruits, plumose seeds, fleshy fruits or nuts, we find bur-reeds (*Sparganium angustifolium, fluctuans*, etc.), pondweeds (*Potamogeton epihydrus, angustifolium, Richardsoni*, etc.), Iris (*I. versicolor*), Pale Corydalis (*C. sempervirens*), vetchlings (*Lathyrus palustris, ochroleucus*, etc.), touch-me-nots (*Impatiens pallida* and *biflora*), violets (*Viola pallens*, etc.), buckbean (*Menyanthes trifoliata*) and the thousands of other species, both vascular and cellular, which make up the aggregate flora of the Canadian Zone. Obviously, this great Canadian flora covering a region, one-fourth of North America, which was available to plants only within thousands, rather than millions, of years, has not taken four times 1½ millions of years (as Willis's estimate for a wind-dispersed tree would require) to become a series of associations in tolerable equilibrium.

The Canadian flora is also a direct refutation of Willis's assertion that "The hypothesis of youth (within the country) and area can only be accepted if one be prepared to accept with it the numerous absurdities to which it leads. It is very far-fetched, with no facts to

rest upon" (82, p. 198). The Canadian flora in a few thousand years has completely occupied an area of 1 to 4½ million square miles. This is not an absurdity nor even a hypothesis but a very plain fact; yet it involves plenty of "youth (within the country) and area" as well. If this simple case seems "far-fetched with no facts to rest upon" I can supply a dozen other cases, taken from the floras of Europe or other regions.

IMAGINARY DATA

It is quite clear, then, that many of the concepts with which Willis works are imaginary. Other botanists and zoologists, likewise, have found them so. Thus, Schonland finds that "Willis is fighting imaginary foes" (68, p. 454), and that in South Africa, as elsewhere, "In many cases the relation of 'Age and Area' can be *surmised*" (68, p. 462) without the intervention of a mathematical formula. And Holmes (46, p. 79) points out that Willis requires a world in process of being stocked with new species and not one in which old ones pass out as new ones come in, saying: "It is absurd to suppose that species . . . . can expand and expand according to Age and Area without causing some unfortunate species of the region to retire"; and concluding: "When we attempt to make what Professor Tyndall calls the scientific use of the imagination in order to see where Dr. Willis's theory of species forming takes us, we find that we are led to a *reductio ad absurdum*."

Ridley regrets "that Dr. Willis seems to base so many of his arguments on statements made in books rather than on observations made in the field" (65, p. 567) and he gives numerous instances of erroneous deductions made from the data thus derived. He also emphasizes the fact that Willis's deductions regarding the plants of Ceylon were based upon the representation of specimens in the Ceylon herbarium and had little to do with their actual rarity or abundance on the island. Both these objections are of far greater importance than the student who approaches the question from a purely theoretical standpoint is likely to realize. With only a few systematists working in a region the tendency, naturally, is to collect and preserve for study the interesting and rare rather than the commonplace species, and it is an oft-repeated truism that an herbarium or a museum is a collection of the exceptional rather than the ordinary forms. Any large collection illustrates this point. The Curly Grass (*Schizaea pusilla*) makes a dramatic appeal to a botanist of the northern hemisphere because it is the only species north of the Tropics of a prevailingly austral and ancient group; but the Cinnamon Fern (*Osmunda cinnamomea*) stirs no enthusiasm in the collector in eastern America. Consequently, we find in the Gray Herbarium 15 collections from Nova Scotia of the Schizaea from an area in the province 320 miles long, while the Osmunda is represented by only 6 collections from a much smaller area. By the method used by Willis the former would be called "common" or "very common," the latter "rare," but every child through the length of Nova Scotia knows the Osmunda, and it is safe to state that the only Nova Scotians who have ever seen *Schizaea* growing are those to whom Messrs. Nichols, Long or I have shown the plant. To be sure, Willis emphasizes that "my figures . . . . refer to area occupied, not to commonness on the ground" (82, p. 192), to which statement Bateson pertinently replied that "the area 'occupied' by a species has immediately to be explained as meaning the area over which the

species *extends*" (4, p. 39); but even allowing, for the moment, that the "area over which the species extends" and not the "commonness" is of most importance, it must be obvious that the working out of "area" merely by the abundant representation of rarities in herbaria and the scant representation of the common species leads to the recognition of the "very rare" as *common*, the "very common" as *rare*. Surely the wholesale piling up of such errors must vitiate the result.

IMAGINARY SUPPORT

Willis seems to see in any one who mentions age, time, space or range in connection with plants or animals a supporter of Age and Area. Thus he attempts to show that two of the greatest men of the last century, Sir Charles Lyell and Sir Joseph Hooker, had really "discovered" Age and Area, simply because Lyell stated, and Hooker subscribed to the statement, that:

> As a general rule, ... species common to many distant provinces, or those now found to inhabit very distant parts of the globe, are to be regarded as the most ancient. Numerically speaking, they may not perhaps be largely represented, but their wide diffusion shows that they have had a long time to spread themselves, and have been able to survive many important revolutions in physical geography (54, p. 702).

Lyell's statement is comon sense, but it is certainly far from Age and Area with all its implications; and when Hooker specifically said in the passage quoted by Willis, "we may not reverse the position, and assume local species to be among the most recenty created" (47, p. xxv), he squarely opposed the teachings of Age and Area that local species are the youngest. Lyell and Hooker did not have an opportunity personally to disclaim sponsorship for Willis's views, but Tate Regan, the great authority on fishes, did. At the meeting of the British Association at Hull in 1922 there was a general discussion of *The Present Position of Darwinism*. During the discussion Mr. Regan said:

> Dr. Willis has shown on the screen a passage from my book on British Fresh Water Fishes, in which I state that dispersal takes time and proceeds at varying rates according to circumstances. From this he claims me as a supporter of the "age and area" hypothesis. . . . . After careful consideration of the "age and area" hypothesis, I have reached the conclusion that it has no value (62, p. 164).

What could be more flat-footed than that?

UNVERIFIED IDENTITIES

Many accurate systematic botanists besides Ridley have pointed out that, in depending upon what he finds in books, instead of having a personal knowledge of the plants, Willis often falls into error, especially since he so often fails to check the identities with the best recent studies; and such an experienced student of the echinoderms as Clark, pointing out that the term *genus* is very inexact and that in comparing "genera" Willis often compares mixed elements, says: "I can juggle the genera of echinoderms . . . . so as to lend apparent support to the Age and Area hypothesis, or I can redefine them so as to contradict it strongly, and in either case I can quote high authorities or give excellent reasons for my course" (17). One other instance of the need of accurate identification and correlation of groups before making sweeping deductions may be noted. In the passage quoted by Willis (91, p. 4) to indicate that Hooker was an early "discoverer" of Age and Area, Hooker said:

> If this be true, it follows that consistently with the theory of the antiquity of the alpine flora of New Zealand, we should find amongst the plants common to New Zealand and the Antarctic Islands

some of the most cosmopolitan, and we do so in *Montia fontana*, *Callitriche verna*, *Cardamine hirsuta*, *Epilobium tetragonum* and many others.

Now everyone knows that Hooker drew his species with very broad limits and in 1853 he was more conservative as to specific lines than in his more experienced years; and, now, three-fourths of a century since the original statement, all critical systematists know that not one of the species mentioned by Hooker occurs in New Zealand nor (except perhaps the Callitriche in South America) in the southern hemisphere; yet I can find no indication by Willis that the determinations are open to question. *Montia fontana* (*M. minor* Gmel.) is characterized by having dull or opaque, plump back seeds conspicuously and closely covered with acutish to blunt tubercles and it is known only from Eurasia and western North America (see 34, p. 138, and t. 84); the plant of New Zealand, as any one can quickly see by examining New Zealand specimens, has much larger lenticular seeds which are highly lustrous and with flattened or obsolete tubercles. Its identity I do not know. *Cardamine hirsuta* is an annual of the northern hemisphere (chiefly Eurasia), the New Zealand plants which Hooker identified with it being three perennials with strikingly different habits, flowers, seeds, etc.; and so on with the Callitriche and the Epilobium. The New Zealand plants are *Montia* sp.; *Cardamine corymbosa* Hook. f. (Sir Joseph), endemic to New Zealand and Campbell I., *C. glacialis* (Forster) DC., of the antarctic and subantarctic regions, and *C. heterophylla* (Forster) O. E. Schulz (*C. debilis* Banks), of New Zealand and Chatham I. (see O. E. Schulz, Mon. Gatt. Card.); *Callitriche antarctica* Engelm. of the antarctic area and *C. Muelleri* Sond. of Australia, New Zealand and neighboring islands; and *Epilobium Billardierianum* Ser. of Australia, Tasmania and the New Zealand region (see Haussknecht, Mon. Gatt. Epil.). In his *Flora of Stewart Island (New Zealand): A Study of Taxonomic Distribution* (86), Willis naïvely lists many other pseudo-cosmopolitan species. The New Zealand plant is assuredly not *Elatine americana* (see Fernald, Rhodora, xix, 12) but is presumably *E. gratioloides* A. Cunn.; the *Hydrocotyle* "*americana*" of New Zealand is the endemic *H. heteromeria* A. Rich.; the *Crantzia* "*lineata*" of New Zealand is utterly unlike the true *Crantzia* or *Lilaeopsis lineata*, which occurs strictly on the Atlantic coast of North America (see Fernald, Rhodora, xxvi, 93); the New Zealand representatives of the Eurasian *Luzula campestris* are the endemic *L. Banksiana* E. Meyer, *L. australasica* Steud. and others endemic to the Australasian region (see Buchenau in Engler, Pflanzenr. iv[36], 90–93); the plant of New Zealand which has long passed as *Potamogeton polygonifolius* is the endemic *P. subollongus* Hagström (Crit. Researches on Pot. 182); *Festuca rubra* probably does not occur in New Zealand (see Hackel, Mon. Fest. Eur. where the extra-European range excludes the southern hemisphere); *Pteris aquilina* of New Zealand is certainly not the plant of Eurasia but, as everyone knows, is *P. esculenta* Forst. or, if you wish, *P. aquilina*, var. *esculenta* (Forst.) Hook.; and the New Zealand representative of *Polystichum aculeatum* is the wholly different *P. vestitum* (Forst.) Presl (See Christ, *Ueber die australen Polystichum-Arten*, Arkiv för Bot. iv, no. 12). Other cases, like those of *Spergularia media*, *Juncus effusus* and *Deschampsia cespitosa*, groups with sharply defined geographic segregates. I have not attempted to check, but any critical systematist will realize, without argument,

that the New Zealand plants will prove quite distinct from the European. With 100 per cent of error in Willis's identifications of such plants of New Zealand as I happen to know something about, what hope can there be that all the other reputedly wide-ranging species would pass unchallenged a critical systematic inspection? In other words, to resume the original thread, not one of the four European species mentioned by Hooker (and after him by Willis) occur in New Zealand, but they are there represented by species endemic to New Zealand or to the subantarctic region. If as "cosmopolitan" species they demonstrated by their broad ranges in New Zealand the truth of Age and Area, do they now as endemic or near-endemics suddenly restrict their ranges in New Zealand? In almost the same paragraph Willis says: "I must consider myself very fortunate in having finally discovered that the effects of age were sufficiently clear to be arithmetically expressed" (91, p. 6). As an illustration of mathematics applied to problems of plant distribution, the occurrence of "cosmopolitan" species in New Zealand, involving an error of 100 per cent, is unfortunate.

INACCURATE GEOLOGICAL DATA

Other features of Willis's work which at once demonstrate that no reliance can be placed upon the precision of his method and consequently upon the soundness of his deductions are numerous. One case in particular is very pathetic or very ludicrous according to the degree of compassion one may feel. Professor James Small contributes a chapter on *Age and Area, and Size and Space, in Compositae*, in which he develops his ideas of the evolution of the group. Because of the great expansion of the genus *Senecio* in the northern Andean region he localizes the evolution of the Composites through that genus in the Andes in upper Cretaceous time. But, as Berry remarks, the fact that Small "by age-and-area methods, finds that the great alliance of the Compositae originated in the mountains of northwestern South America at a time when there were neither mountains nor even land in that region, but seas, does not add to my confidence in the general method" (7, p. 547); and Bateson politely said: "The inclusion of the chapter on the Composites reflects more credit on Dr. Willis's candor than on his scientific judgment" (4, p. 41). The fact is, that the great elevation of the Andes, where *Senecio* now has its phenomenal development, did not occur until the Pliocene and early Pleistocene (69, p. 923; 6, p. 8); and, although Willis finds Small's work a "remarkable verification" (91, p. 116) of Age and Area, opponents might be tempted to point out that, since it is based on a colossal error, it is *naturally* a verification of Age and Error!

WILLIS'S COLLABORATORS

A chapter is contributed by de Vries, who finds Willis's work "the one great proof, which the mutation theory still wanted for its acceptance in the field of systematic zoology and botany" (91, p. 227). Nevertheless, I have seen no indication of the systematic zoölogists and botanisis swinging in a body to the mutation theory! Guppy has a short chapter in which he discusses the *Position of the Age and Area Theory;* and Mrs. Clement Reid, although admitting that "the evidence of universal extinction of species furnished by the pages of palaeobotany is incontrovertible" (91, p. 143) and that "more species found in the older deposits are extinct, than in the newer" (91, p. 144), stands almost if not quite unique among paleontologists

in conferring her benediction on Willis's views.

PREDICTIONS BY AGE AND AREA

As to the reiterated insistence by Willis that all his provisos must be kept in mind, but that in spite of their negating tendency Age and Area is a hypothesis by which one may discover new facts, and that *all* predictions made by it have proved to be correct, Bateson justly remarked: "Repetition of the bald assurance that Age and Area is the true faith should be unnecessary. A judicious advocate would leave that conclusion to flow more quietly from the evidence . . . . the reader's scepticism is thus instantly aroused" (4, p. 39). As to predictions made by others, Willis seems to take comfort in the two made in America: "Taylor has studied the endemics of New York and of the Bahama islands, obtaining results that harmonize quite well with the general theory of Age and Area" (91, p. 64). Willis admits, however, that in case of the Bahamas "it was noticed that the difference usually seen between the distribution of the endemics and the wides was not nearly so large as usual." And as to the endemics of the region of New York, the facts are illuminating. Taylor (75) recognized 22 species as endemic to his area. But of these, 1 extends south to Florida, 1 to South Carolina, 1 to North Carolina, 2 to Virginia, 1 to Maryland, 1 beyond Taylor's limits in Pennsylvania and 1 eastward to Rhode Island; 2 are apparently local hybrids and 1 (*Salix squamata*) was simply an aberrent individual of the wide-spread *S. discolor*. These rejected "endemics" of the New York region are as follows: *Calamovilfa brevipilus* (North Carolina acc. to Hitchcock, Gen. Grasses U. S. 125); *Juncus caesariensis* (Virginia, Grimes, Rhodora, xxiv, 149); *Uvularia nitida* (South Carolina, as the scarcely separable *Oakesia puberula* acc. to Robinson and Fernald, Gray Man. ed. 7, 286); *Salix squamata* (see Schneider, Journ. Arn. Arb. ii, 3); *Dentaria incisifolia* and *D. anomala*, strongly suggesting hybrids, the latter thought by its author to "have had a hybrid origin" (Eames, Rhodora, v, 217); *Prunus alleghaniensis* (see Taylor, Torreya, xvi, 18); *Hibiscus oculiroseus* (Rhode Island, Sanford, Rhodora, xxvi, 88); *Ludwigiantha brevipes* (Virginia, *Rugel*, 1840, in Gray Herb.); *Dendrium buxifolium* (Florida acc. to Small, Fl. Se. U. S. ed. 2, 822) and *Senecio Crawfordii* (Maryland, Standley, Rhodora, xxi, 117). That leaves, as endemic to the region within 100 miles of New York City, 2 freakish plants (*Hypericum Bissellii* and *Pyrola oxypetala*) which were exterminated by their discoverers, 3 true endemics of the comparatively ancient Pine Barrens of New Jersey, and 6 localized species occurring at the border of the now submerged Cretaceous and Tertiary continental shelf, the latter region before completely going under the sea having left a relic-flora along the margin of the continent eastward to Nova Scotia and even to Newfoundland (see 28, pp. 149-162; 31, p. 168; 50, chap. viii). These 6 endemics are quite possibly as ancient as those of the Pine Barrens. At any rate, like the endemics of the Bahamas, they are not in any way proof of Age and Area.

I personally spent several weeks in a test of Age and Area, taking for my test two regions upon which I had worked during a quarter-century, Newfoundland and the Gaspé Peninsula. The resulting figures upon superficial examination "seem very reassuring to supporters of Age and Area. . . . . But . . . . the actual facts are squarely opposed to Age and Area; for in both Gaspé and Newfoundland the most ancient flora of each region has the most limited range and also the

most limited 'wide' range, while the youngest flora to arrive in each area has two or three times the range both inside and outside these regions" (32, p. 563). Calvert, likewise, has attempted to get satisfaction out of Willis's method by applying it to the distribution of insects in various regions but finally concluded: "I fail to find the key to the origin and evolution of species with the ease which Dr. Willis's commendation of Age and Area would lead me to expect and which I would welcome if the key but turned in the lock" (13, p. 229).

So much for the general question; now for some of the correlaries and details.

SIZE AND SPACE

Seeking to catch the popular fancy, Willis hit on what he calls his "alliterative series." The trick is an old one but it should not take the place of plain facts and sound reasoning. The ear is quickly caught by such pairs as Age and Area, Antiquity and Amplitude, Rank and Range, Size and Space and Size and Surface, and Willis specially selects "Age nd Area" and "Size and Space" (*alias* "Antiquity and Amplitude") for immortalization. It is worth noting, however, that he is somewhat confused in tracing the relationship of "Size and Space." Sometimes he speaks of it as the child or "extension" (91, p. 113) of "Age and Area," at others he states that "Age and Area" and "Size and Space" are *twins* (91, p. 107). Since Willis, himself, was the only witness of the birth of both of them, it is regrettable that in a question dealing with relative ages such contradictory evidence should have crept in. Willis's statement of Size and Space is:

> Keeping to the same circle of affinity, the larger families and genera will be the older, and will therefore occupy the most space. This, however, involves a break with the long current idea, that the larger families and genera are the successful ones, the smaller the (comparative) failures (91, p. 113).

Or in more concise form he says: "The larger a genus, the older will it be, *within its own circle of affinity*." And, extending his ideas, he applies the same formula to groups of related species and to related families and always finds his own predictions successful. "Species and genera are endemic simply because they have not yet had time to spread abroad" (91, p. 183). "The supposition that endemic genera are usually relics . . . . must be ruled out of consideration" (91, p. 110). Species, according to Willis, originate in regular mathematical progression, each genus or series throwing off a species at a regular interval, and the spread of the species is radial from the center of origin; and he believes that the facts of distribution can be expressed by a "hollow curve."

> The hollow curve is apparently a universal principle of distribution, whether it be distribution in space—geographical distribution—or distribution in time—evolution. A species as it increases in age expands its area, while a genus increases its number of species, the younger occupying smaller and smaller areas, usually within the area of the first species, until that becomes very large (91, p. 199).

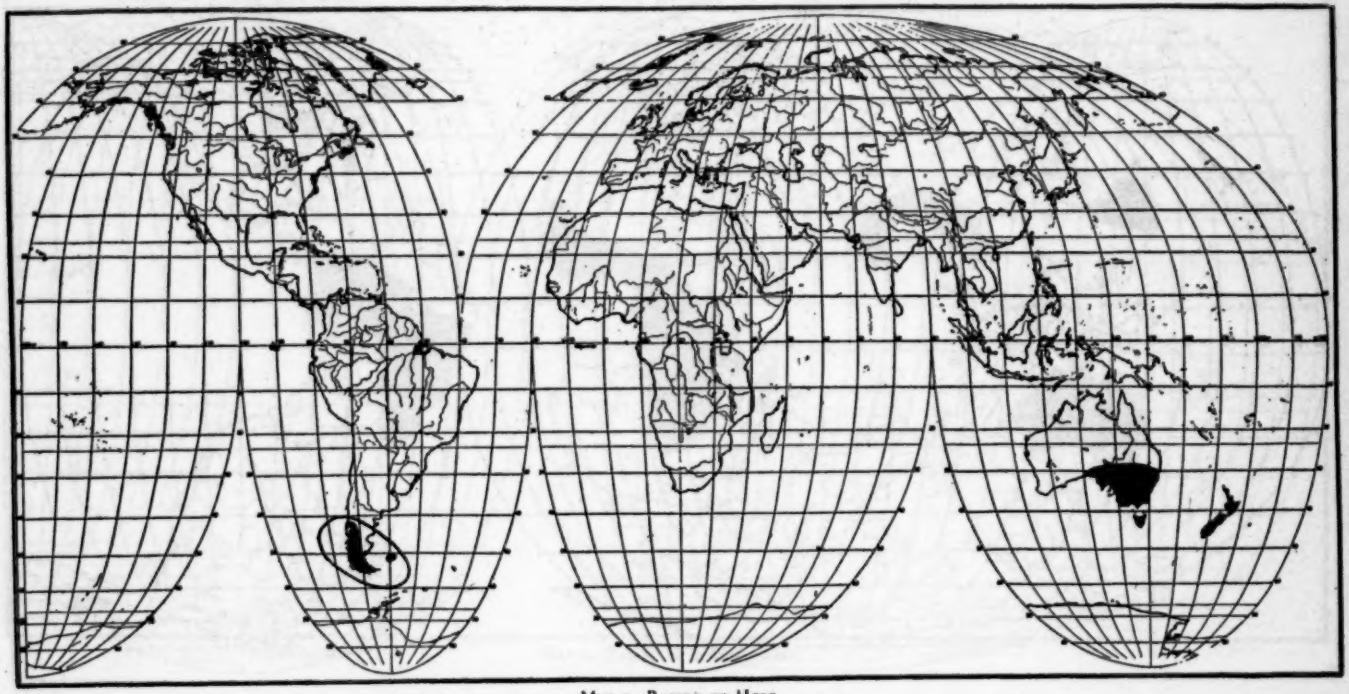
REFUTATION BY PALEONTOLOGY

It is thus again obvious that Willis and his mathematical friends live in a theoretical world and that, although going through the form of admitting geological, ecological and climatic changes, they do not really comprehend how vast and all-controlling the actual historic and edaphic factors have been. Immediately they were confronted by the paleontologist, and such an unchallenged authority as Seward pointed out, that in the "confers and ferns, study showed that the forms existing now in restricted areas were the oldest and not the youngest"

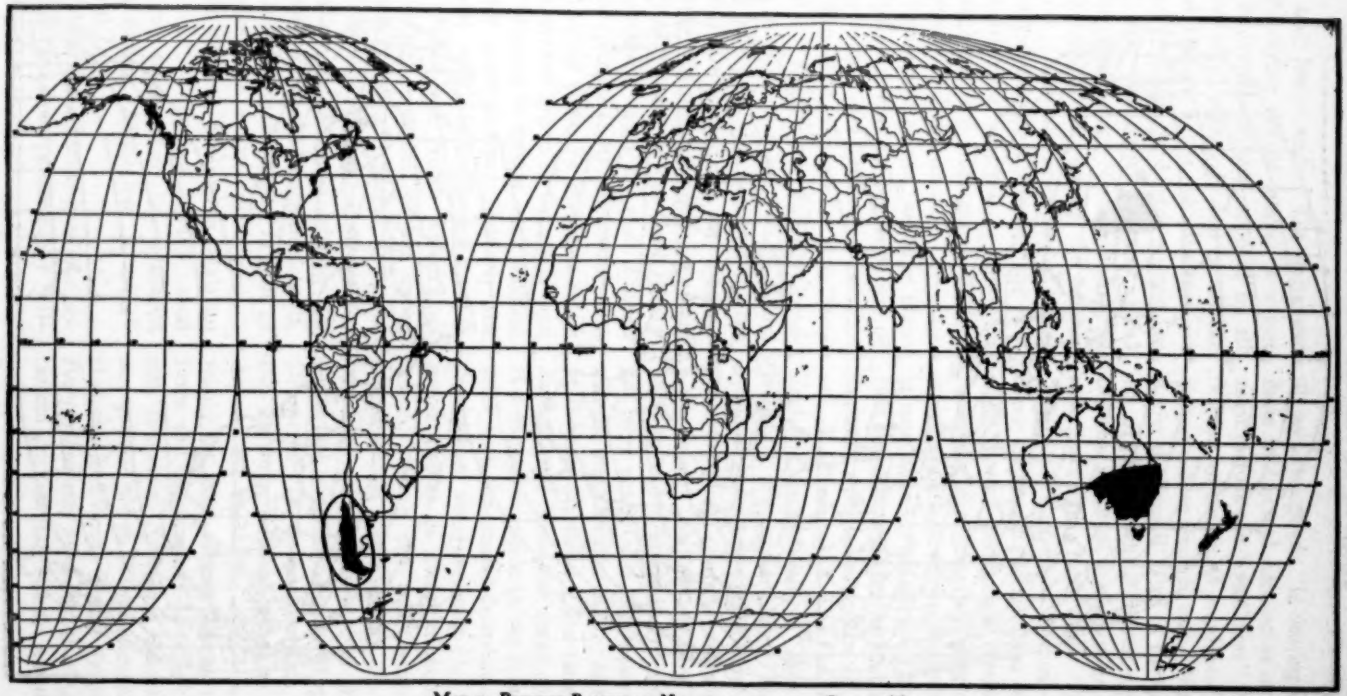
(70); and Berry said: "The statement that the dying out of species is a rare event is overwhelmingly opposed by all the facts of paleontology and by all the facts of history unless its adherents are prepared to accept the Mosaic cosmogony . . . . the probability is very great that the present flora of the globe represents a minute fraction of the extinct floras . . . . in all the orders of plants that are prevailingly aborescent the geologic distribution where it is known is found to have been more extensive than the present distribution. . . . . So-called monotypic genera, whether plant or animal, at least in the majority of cases, are relicts of a once wider distribution" (5, p. 540). Somewhat later Berry amplified his statement by publishing convincing maps of past and present ranges of many genera (6, 7). Ridley, along the same lines, also pointed out, that the most extensively distributed flowering plant in the world today is the Reed, *Phragmites communis*, with a *good dispersal mechanism* (plumed fruits) but unknown as a fossil earlier than the Pliocene; while the vast ancient group of Cycads is now reduced to about 80 species, each confined to a very limited area. Similarly the Nipa Palm, which in the Eocene grew in Europe, Africa and North America, is today confined to shores of "the Indian Ocean from Ceylon and Bengal, down the Malay Peninsula to North Australia and the Caroline and Solomon Islands, not having got so far as the Mascarene Islands, peninsular India, or Polynesia, in spite of its abundance as a drift plant . . . . always to be seen drifting in Malayan seas. It . . . . requires tidal mud . . . . but there must be tidal-mud rivers in Samoa, Africa and America" (66, p. 29).

But to these and all other parallel cases brought forward from paleontology Willis merely replied: "in dealing with them from an Age and Area point of view, one must include the 'fossil' area" (91, p. 94).

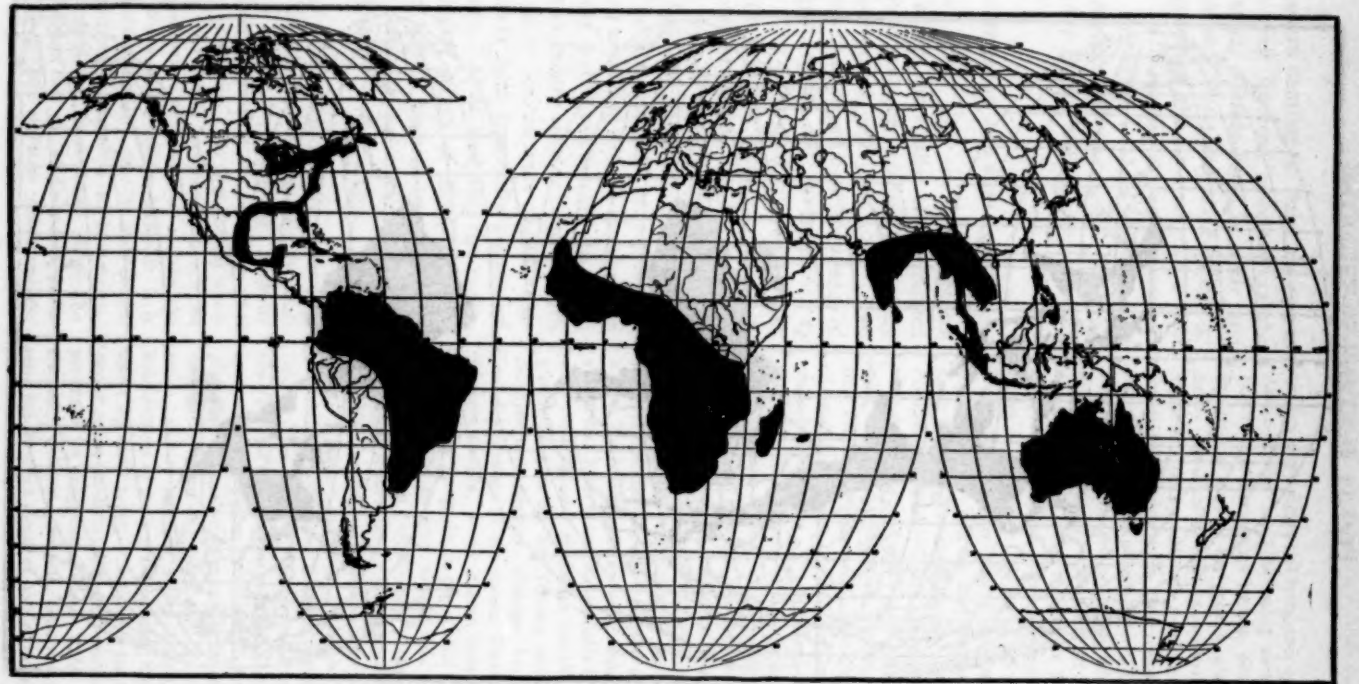
That, of course, is a quibble, as has repeatedly been pointed out. How can we know the "fossil" area of the vast majority of plants, which, occurring today as obvious relics of former wide dispersal, must have had a fossil area? The woody "Veronicas" of New Zealand differ in every important detail from the essentially boreal herbaceous Veronicas and constitute the genus or subgenus *Hebe*, which has characters more primitive than in true *Veronica* (see 59, p. 2; 32, p. 571). *Hebe* has most of its present species in New Zealand, with a few species in Australia and Tasmania, and four of the New Zealand species also on the Falkland Islands or in southern Chile. The present range of *Hebe* (map 2) is almost identical with the range of such genera as *Nothofagus* (map 3), whose ancestry is traced back to the Cretaceous (6, chap. xii), and very nearly that of *Araucaria* which extends much farther back; yet no fossils of *Hebe* are identified. The ranges of the *Eriocaulaceae*, *Xyridaceae* (map 4) and the *Halorrhageae* coincide in their larger features with the present distribution of the Persimmon, *Diospyros* (map 5). "In that grand display of dicotyledonous genera which, during the mid-Cretaceous replaced the old Mesozoic flora . . . . we find unmistakable evidence of the abundance and wide distribution of species of Diospyros" (6, p. 257), which covered the northern hemisphere quite to the Arctic. He would be a bold man who would say that, simply because they are herbs and consequently have left no fossils, *Eriocaulon*, *Xyris* and *Halorrhagis* are not quite as old as *Diospyros;* or, similarly that the herbaceous genera *Symplocarpus*, *Podophyllum* and *Mitchella*, sharing southeastern continental North America and



Map 1. Range of Hebe



Map 3. Present Range of Nothofagus, after Berry (6)



Map 4. Range of Xyridaceae

Map 5. Present Range of Dicotyles, after Brett (6 and 7)

southeastern continental Asia, are not as old as their ligneous associates in the same areas, *Liriodendron*, *Sassafras* and *Liquidambar*. These and many other ligneous genera of the same ranges are well known as Mesozoic or early Cenozoic types. But what is the fossil range of their herbaceous associates? We can safely infer it but, after all, we can only infer it.

AGES OF LARGE AND SMALL GENERA

Willis's idea, that the larger genera are the older, the smaller closely related genera the younger, gathers force only by his perpetual repetition of it. But those who have an intimate knowledge of the morphological and phylogenetic, as well as the geological evidence make exactly the opposite decision. The paleontological evidence is decisive; the evidence from living groups is quite as good. The very numerous genera which formed the Mesozoic and early Cenozoic flora, then extending around the northern hemisphere but now reduced to small remnants in eastern Asia or eastern North America or to limited areas on both continents, have been repeatedly marshalled as evidence. After studying the ranges of the largest genera of dicotyledons of temperate North America in relation to Age and Area I summarized my conclusions as follows:

> Now, by Willis's interpretation these large genera are large because they are old, the small genera small because they are young. Naturally there is no *absolute* proof of this or of any other hypothetical proposition. But does not the whole matter leave the realm of hypothesis and enter the realm of demonstrable fact when we consider the geological history of the regions involved? It is generally conceded, I believe, that the most ancient living floras are now concentrated largely in Australia, New Zealand and South Africa. It is also generally admitted that the Mediterranean basin, including a broad belt of North Africa and the country across Egypt and Syria, and, again, the great Austro-Russian basin extending southeastward to Persia were Tertiary sea bottom; similarly, by far the greatest part of the prairies, plains, and arid basins west of the Mississippi owe their present condition to Tertiary and even more recent geological activities. In other words, these regions were largely unavailable to their present floras millions of years after most of the groups which now distinguish Australia and New Zealand were at the height of their development. If, then, the largest genera of our flora, which are also overwhelmingly the largest genera of their own "circles of affinity," are, as Willis maintains, large because they are the ancient genera, is it not singular that *Eriogonum*, *Crataegus*, *Rubus* § *Eubatus*, *Lupinus*, *Astragalus*, *Oenothera*, *Gilia*, *Phacelia*, *Pentstemon*, *Solidago*, *Aplopappus*, and *Artemisia* should have not even a single species associated with the ancient types which inhabit Australia and New Zealand, and that only 0.01 of the total species of *Potentilla*, *Euphorbia*, *Aster* and *Erigeron* should have reached those lands? Is it not equally noteworthy that, with the exception of *Crataegus* and the blackberries (*Rubus* § *Eubatus*), all the *largest* genera of the temperate North American flora should be centralized upon the Tertiary sea bottoms (relatively youthful country) of the Mediterranean and Austro-Russian basins of the Old World and in the vast area of youthful country west and southwest of the Mississippi? The blackberries are most virulent in central and western Europe, a region available to plants only since the Pleistocene glaciation, but likewise in the glaciated region and the Tertiary coastal plain of eastern North America. *Crataegus* has its phenomenal development in the eastern United States and southern Canada, where it must have produced a multitude of its species in post-glacial time.
>
> It should be perfectly obvious that these genera and likewise such overwhelmingly large genera of Europe and southwestern Asia (but not of Australia and New Zealand) as *Dianthus* (200–300 Eurasian species), *Silene* (300–400), *Verbascum* (150–200), *Cousinia* (150), *Centaurea* (200–300), and *Hieracium* (600–700) are really very young, or, if geologically old (*Crataegus* and *Rubus* for example), they have been encouraged by modern conditions to rapid multiplication. And if we estimate success of plants by their ability to cover country, to take care of themselves, and to multiply their variations to the bewilderment of the best systematists, then these are surely successful genera. No society for the protection of native plants has thought it necessary to urge protection for *Eriogonum*, *Crataegus*, *Rubus* § *Eubatus*, *Euphorbia*, *Solidago*, *Artemisia*, *Centaurea*, and *Hieracium;* but there are plenty of people (including many

botanists) who would be glad to have them suppressed.

The genera of eastern America which need scrupulous protection are the woodland herbs of the Alleghenian forest, the genera which we largely share with Japan and China and which are consequently among the oldest plants now living on the North American continent. These are chiefly ditypes, with one species in eastern America, one in eastern Asia, though some of the genera have more than two species; but, while the systematist shrugs his shoulders and waves you away if you bring him for determination a collection of the youthful species of *Lupinus*, *Oenothera*, *Aster*, or *Artemisia*, he can give a prompt and explicit determination of *Caulophyllum*, *Podophyllum*, *Dicentra*, *Panax*, *Cryptotaenia*, *Epigaea*, *Chiogenes*, and *Mitchella*—and why should he not? These are genera of the eastern Asiatic-eastern American forests; and they are absolutely segregated genera with no complications of freely intergradient species, not, as Age and Area asserts, because they are young beginners, but because they are old veterans (32, pp. 568–570).

If these cases are not conclusive, let us consider the tribe *Caricetae* of the Sedges. Kükenthal (53) recognizes four genera. *Carex* is world-wide, with 798 species, which in view of more recent studies can safely be extended to 850. *Uncinia*, with 24 species, is on the subantarctic islands (the Falklands, Sandwich Islands, Amsterdam I., Tristan da Cunha, Kerguelen, St. Paul, Macquarie, Auckland and Campbell) thence extending north into South America, New Zealand, Australia and New Guinea. North of New Guinea in the East and of South America in the West the genus is unknown except for 1 species found the length of South America and slightly northward into Costa Rica, another extending from South America to Mexico and Jamaica; but the problematic *Carex microglochin* Wahlenb. (described from mountains of arctic Lapland) is so poorly distinguished from *Uncinia* that one of the greatest students of the *Cyperaceae*, the late C. B. Clarke, wrote: "I feel sure that, had *C. microglochin* been found in the southern hemisphere instead of in the northern, authors would have placed it without hesitation in *Uncinia*" (18, p. 374). Now it so happens that *C. microglochin*, or a plant scarcely separable from it, actually has been found in the southern hemisphere, in Patagonia and Fuegia (18, p. 402; 53, p. 109); and in the northern hemisphere it has the thoroughly typical disrupted range of a relic-species, chiefly in areas whose floras were not destroyed by the latest advances of the continental ice-sheets of the Pleistocene. The third genus is *Kobresia*, with 29 species, 27 of them confined to the ancient flora of Asia, the other 2 also found in Asia but also with a highly disrupted relic-distribution around the northern hemisphere; and the fourth genus is *Schoenoxyphium*, with 6 species all endemic to South Africa.

Now by Age and Area, the vast genus *Carex* (850± species) is the oldest of the four because today it is world-wide and overwhelmingly the largest group; *Uncinia*, *Kobresia* and *Schoenoxyphium* should be very much younger because they are more localized and with far fewer species. Nevertheless, no critical student of the group hesitates for an instant in believing that the presence of the rachilla (the axis of a spikelet such as is found in most sedges) in all three of the small and localized genera and the mostly open spathe in *Kobresia* and *Schoenoxyphium* are primitive characters; and that the great bulk of true *Carices*, in lacking the rachilla (having the female spikelet reduced to a single flower) and in having the margins of the spathe united to form a closed pouch (the perigynium or utriculus), are later in origin than the other three genera.

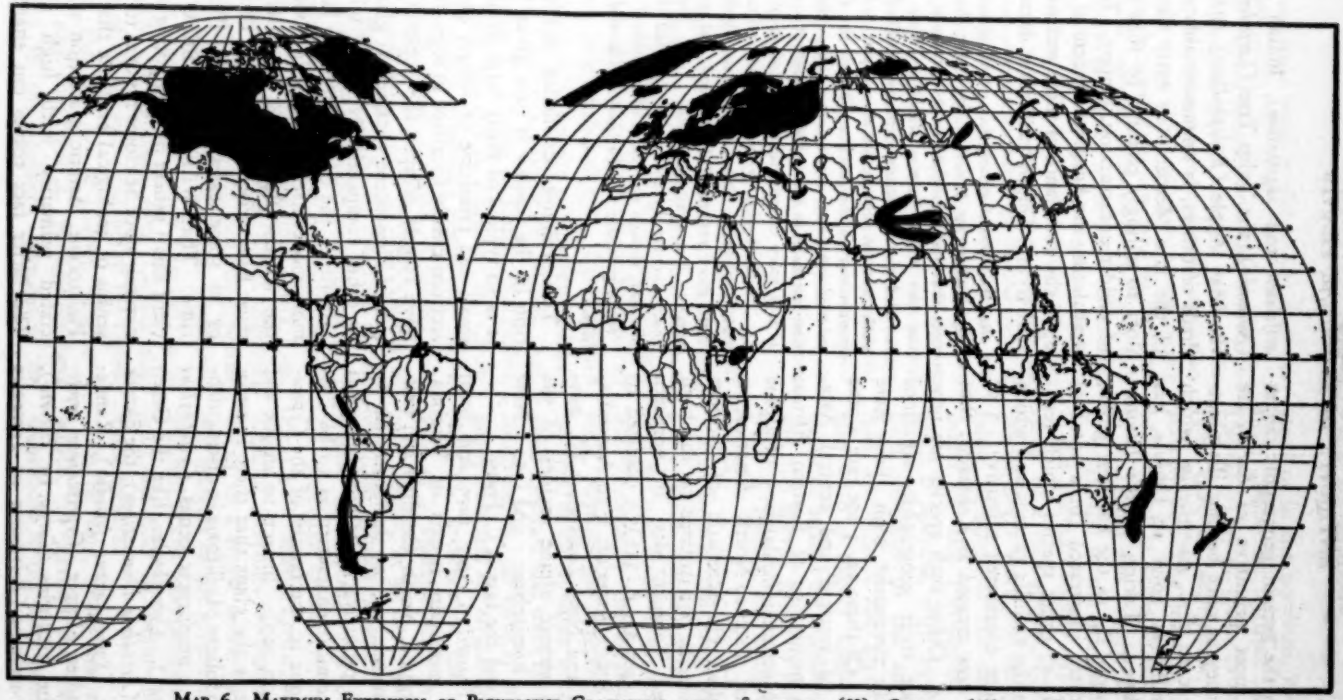
To be sure, there are a few *Carices* which, in having the rachilla, show transitions to the more primitive genera;

but, when the present geographic ranges of these most primitive of *Carices* are checked, they at once become illuminating. The case of *C. microglochin*, which is practically as good an *Uncinia*, has been discussed. Taking Boott's *Illustrations of Carex* (11) as the handiest guide, we find there illustrated (in a total of 600 plates) 17 other species which regularly have the rachilla present and which are therefore considered primitive. 3 of these are now treated as Kobresias; thus leaving 14. Other such species are now known but their geographic isolations are wholly consistent with those here discussed. Of these 14, 3 are rare alpine endemics of western and central Asia, 1 of high mountains of Eastern Africa, 1 of the Macronesian islands, 1 of alpine regions of Pacific North America; 1 (*C. filifolia*) characteristic of western North America but isolated on the high unglaciated Torngat Mts. of northern Labrador (see 33, p. 316); 3 confined to southern South America; 2 to Australia, Tasmania and New Zealand; 1 (*C. pyrenaica*) to remote alpine regions of the northern hemisphere and to New Zealand, and the last is *C. Fraseri*.

Carex Fraseri, a very rare and local plant of mountain woods of Virginia, West Virginia, North Carolina and eastern Tennessee, is, as demonstrated by Holm, so primitive in its morphological and anatomical characters as to be "almost unique in the family of the *Cyperaceae*" (45, p. 127). In fact, so unique and primitive is the plant that there is every reason to follow Mackenzie in distinguishing it as a monotypic genus, *Cymophyllus* (55, p. 441). *Cymophyllus*, like the Green Dragon (*Arisaema Dracontium*), the Skunk Cabbage (*Symplocarpus foetidus*), Ram's-head Ladies Slipper (*Cypripedium arietinum*), the hickories (*Carya* or *Hicoria*), the tear-thumbs (*Polygonum* or *Tracaulon arifolium* and *sagittatum*), Indian Lotus (*Nelumbo*), the Tulip Tree (*Liriodendron*), the May Apple (*Podophyllum*) and hundreds of others, is unquestionably a relic of the late Mesozoic or early Cenozoic flora so tellingly pictured by that master of vivid reconstruction, Guppy. In congratulating the American student of plants upon the abundance of these ancient types still living, Guppy projects a dream:

> In the woods around him were growing the Liquidambar, the Sassafras, and other shrubs and trees that had flourished in the Mesozoic ages in the spot where he was standing. Their remains crowded the Cretaceous deposits exhibited in the cliffs near by. Specimens of the past and of the present were in his hands. Though the difference in kind was very slight . . . . the difference in time, measured in human lives, amounted to eternity. It is a story of perpetuity rather than of change. . . . . He begins with the cosmopolitanism of such types in the Cretaceous age and he ends with their more restricted distribution and somewhat greater specialization now. . . . . Those old genera become the genera of today; and the genera of today, though the genera of a thousand ages, are "but as yesterday" in the history of flowering plants (42).

This prolonged discussion of the situation in the *Cariceae* is here given because it is so typical of many large groups, the small and primitive or unique genera or sections chiefly localized in regions which have largely escaped the depleting agencies of Pleistocene continental glaciations or other comparatively recent wholesale calamities, the overwhelmingly large and more modern series abounding both with the ancient floras and in those which must have arisen in Pliocene, Pleistocene or in some cases even post-Pleistocene time. That Willis might think the ancient small genera of Asia young would be natural, since he closes his eyes to the consensus of geological evidence that, in the Pleistocene, Asiatic glaciation was associated primarily with high altitudes. The latter fact comes out sharply in a



MAP 6. MAXIMUM EXTENSION OF PLEISTOCENE GLACIATION, AFTER SCHUCHERT (69), GRABAU (40) AND FERNALD (33)

map of the maximum Pleistocene glaciation of the northern hemisphere (map 6) Willis, ignoring such evidence, speaks without a word of qualification of "China, where the influence of the last glacial period was severely felt" (91, p. 88). Naturally, if one ignores all geological and morphological facts, he can at will prove anything either young or old; but that Guppy, who wrote the pregnant passage above quoted, should give his approval to Age and Area is certainly amazing.

Another case, which Willis cites, is instructive. Taking the 28 largest genera in the world, Willis states that 16 are cosmopolitan, 5 cosmo-tropic, 4 tropical American, "and *Quercus* Old World [surely *Quercus* grows in the New World, Trelease (77) recognizing 372 American species], leaving only *Erica* and *Mesembryanthemum*, whose large number of species is correlated in both cases with the fact that they grow in South Africa, where the extreme conditions [Is this mathematical saltation?] seem to tend to produce large numbers of species" (91, p. 117). Now, in regard to *Erica*, Schonland shows, by a detailed tabulation of the 5 subgenera, 41 sections and approximately 1000 species of the genus in South Africa, that "the whole theory [of Age and Area] as applied to this case tumbles to pieces—(1) When we analyze groups of species; (2) when we take into account allied genera which appear to be derived from the genus *Erica;* (3) when we take into account the distribution of the *Ericaceae* generally, and of *Erica* in particular, which seem to prove that *Erica* has arisen in the Northern Hemisphere. There is not a single fact known which indicates southern origin. It must have come to us through the mountains of tropical Africa." And, after discussion of the details, Schonland says:

> Most of these remarks were excerpted by me some time ago, without any idea of proving or disproving a theory. They show, however, plainly in the first place that when we come to bed-rock of Willis's "Age and Area theory" by comparing a number of closely allied species of the same ecological type, the present distribution of the South African species of *Erica* does not fit in with a mechanical rule such as Willis thinks he has discovered as governing the distribution of plants. The species which occur at widely separated stations or closely allied species in similar position, both of which will be found in these brief remarks, are particularly interesting, as previously pointed out, because if they disappeared from either of their distant stations their whole position in a scheme of distribution would be completely altered. . . .
>
> When we come to the tropical African species we again find little to help us in gauging age by area. . . . .
>
> Before further commenting on these facts we must glance at the distribution of African genera allied to *Erica*. . . . . The huge gaps in the distribution of these derived genera are particularly noteworthy. If we knew the genus *Erica* and its allies only, we might come to the conclusion that it has dwelt longest in South Africa and that all species outside South Africa are outliers. Thus we would assume that the development has taken place in a northward direction. This assumption probably would to a certain extent be correct, but on considering the other *Ericaceae* we see that the original current of distribution has been in just the opposite direction. However, no "Age and Area theory" can disentangle these two opposite currents except in the vaguest sort of way. Willis, "with the aid of a prediction of the bearings of Age and Area upon the subject," came to the conclusion, as regards the New Zealand flora, that the number of endemic species in any genus would rise "gradually to a maximum at or near the point where the genus entered New Zealand in the first place." Applying this prediction to the genus *Erica* in South Africa, this point would be a part of South-west Cape Colony west of George, where not only a large number of endemics are massed, but where, moreover, the greatest diversity owing to formation of subgenera and derived genera is to be found; but I fear no contradiction when I assert that it is certainly not the place where the genus *Erica* entered South Africa, or where it originated, and thus again Willis's theory breaks down (68, pp. 465–471).

AGES OF ENDEMICS

In regard to Willis's idea that the endemic genera and species are young beginners, it has been repeatedly pointed out that there are two kinds of endemics:

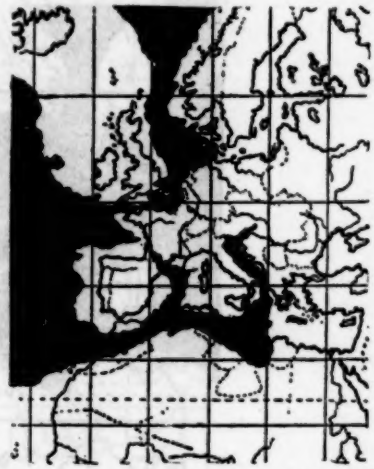
those which occur in the neighborhood of their allies, for which Ridley would retain the term *Endemics* "which signifies those who live with their people"; and those which are far removed geographically from their allies, the survivors of a lost flora, for which he proposes "the name *Epibiotics*, which signifies survivors" (67). The former or true endemics are naturally younger than their ancestors. No one questions that. Whether they are more numerous or less numerous than the epibiotics I cannot say. Willis says they are more abundant and certainly the vast numbers of somewhat localized species of *Astragalus*, *Artemisia*, *Crataegus*, *Rubus*, etc., give support to his contention; but these are surely very young species. In fact, some botanists question whether they are species at all or whether they will reach sharp specific segregation within the era of human history. Such groups as these will be further discussed in another connection.

In many floras a large proportion of the genera, although not themselves endemic genera, are represented only by endemic species. Willis maintains that these are young species, which have been given off by some wide-ranging species which was the first of the group to arrive on the ground. This situation has been specially noted for New Zealand, where 43 per cent of the genera are said to be non-endemic or wide-ranging genera which in New Zealand are represented only by endemic species. Since Willis's theory states that the species which have a wide range outside a given country will also have a wide range in every country they inhabit (because they are assumed to be the oldest), Sinnott (73, p. 575) raises and pushes the query: What has become of the wide-ranging species of nearly half the genera of the New Zealand flora which were the first to arrive there? If they ever did arrive, they are now completely "swamped out" and Willis's theory, that they must now be the widest-ranging species in New Zealand, falls completely to the ground.

Willis himself, without seeming to understand them, supplies figures which, checked with the most familiar facts of geological history, completely refute his claims. To be sure, I am aware that his figures cannot always be accepted at their face value, for as I have elsewhere been obliged to point out, "in arguing that there are more endemics in tropical than in temperate regions he makes what would seem a clinching assertion: 'North-temperate America has perhaps 400, but Ceylon alone has 800 endemics, and Brazil perhaps 12,000' (91, p. 89). In view of the 1000 endemic grasses recognized in temperate North America, the 400 Carices, the more than 300 Cruciferae or Umbelliferae, the full 100 Malvaceae, to say nothing of Eriogonum, Crataegus, Astragalus, Euphorbia, and all the rest, the utter folly of attempting to prove anything by such wholly unreliable statistics must be apparent" (32, p. 571). But, even taking his figures as presumably near the facts, we find, for instance, that Great Britain has no endemic genera, Japan 69 (91, p. 170) and that of the latter 54 are monotypes (of a single species) and most of the others ditypes, with only 1 genus having as many as 8 species (91, p. 175). We further find that, "Whilst the largest number and proportions of endemics are chiefly in the more southern countries, there are also large numbers and proportions in several of the northern, *e.g.* in Mongolia, California, the region about the Mediterranean Sea, etc. There are a few endemics on the west coast of Europe, the Alps contain about 200, and Italy about the same; and the Iberian peninsula contains about 800, or

roughly the same as Ceylon" (91, p. 149).

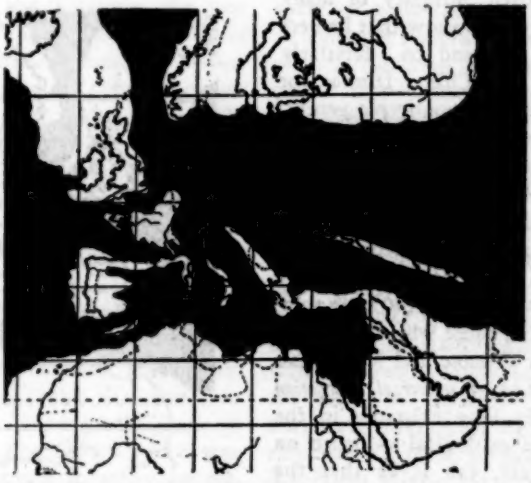
In view of the fact that Great Britain was severely denuded by the Pleistocene glaciers and that, for the most part, her flora has occupied the islands only a few thousand years, it should surprise no one to find the British endemic genera totaling 0; but Japan, undisturbed during the Pleistocene, has 69 endemic genera, mostly monotypes. Yet Willis calls the monotypic genera young, because they have only 1 species. It needs no argument, in view of the proved antiquity of many Japanese monotypes, to show that he here has no ground to stand on. Similarly with Mongolia and China, famous for their great number of monotypic genera. Willis, as already noted, refers to "China, where the influence of the last glacial period was severely felt," but the statements in regard to the Pleistocene in southeastern Asia, by such geologists as James Geikie (37, p. 697), Schuchert (69, see map 6) and Grabau (40), are sufficient to show that those who ascribe the great number of Chinese and Mongolian monotypes to *lack of universal glaciation* and consequently long existance in the region have the geological evidence on their side. Again, can it be that the antiquity of the Iberian tableland, essentially undisturbed since the dawn of angiosperms, has nothing to do with the occurrence there of 800 endemics? From Cretaceous time (map 7), when an arm of the Mediterranean almost severed Iberia from France, through the Eocene (map 8), when continental Europe was almost obliterated by the sea, through the Oligocene (map 9), when the sea wholly separated Iberia from other lands, on through the Pliocene (map 10), when the surrounding seas of Europe were still extensive, and through the Pleistocene (map 6), when the ice-fields of northwestern Eurasia and the enlarged alpine glaciers to the south united to obliterate the older plants of the continent, the Iberian tableland held its own. Obviously its 800 endemics, including many geographically segregated genera and others related only to groups of the most remote regions of the globe, are as ancient as any plants of Europe. But Atlantic Europe to the north, invaded by sea and ice, has "few endemics." This is precisely what one would expect, not because the flora of Atlantic Europe to the north is old, but because it is so very young.



MAP 7. EUROPE IN LATE CRETACEOUS TIME, AFTER GRABAU (40, P. 805)

The endemics of Japan, China, Mongolia and the Iberian peninsula have certainly had time to spread, but they behave exactly like the ancient endemics (epibiotics) of other regions. They are quite comparable with the species now confined to arctic Norway, arctic Russia, and Nova Zembla in Europe, north of the area invaded by the later advances of the European ice-sheets, and in North America found likewise only outside the areas which were

denuded by the later advances of the ice. These older species in America "have long since passed their period of aggressiveness. Left undisturbed they persist in their old habitats, but they fail to move into new and immediately neighboring territory." Similarly "in Scandinavia, where the de-glaciated Scandinavian alps offer most attractive habitats for them, they have rarely ventured out of the limited areas in which they were held trapped through the whole of Pleistocene time" (33, pp. 244, 246).



MAP 8. EUROPE IN EOCENE TIME, AFTER GRABAU (40, p. 811)

Further arguing that endemics are young beginners which have not yet had time to spread, Willis cites the case of *Christisonia albida*, a saprophytic angiosperm of Ceylon, which was exterminated by its discoverer; and in extenuation of that catastrophe he adds: "it is probable that the white colour alone would have been such a disadvantage as to ensure its extermination by nature in any event" (91, p. 151). Nature, then, has wholly neglected her duty with the ghost-white Indian Pipe or Corpse Plant, *Monotropa uniflora*. As a general rule the late Mesozoic and early Cenozoic types, which have lingered in southeastern Asia and in southeastern North America, have quite disappeared from the Pacific slope of America; but, in case of the Indian Pipe, Nature, far from exterminating it, has allowed it to become a common woodland plant throughout eastern America and from Japan and Corea to the Himalayas, and she has even allowed it to remain on the Pacific slope, in Washington, Oregon, and California. Whiteness in saprophytic angiosperms is unusual but it is not necessarily fatal, and in saprophytic agarics it is common. It is surmised that the extinction of *Christisonia albida* is readily explained by the destruction of the forests of Ceylon emphasized by Ridley (65, p. 559) and admitted by Willis (82, p. 191).

Finding that a large proportion of endemics in Ceylon were confined to solitary small areas on the mountain summits (just as in other mountainous regions), Willis, opposing the general interpretation that such species are survivors,

dramatically asked: "Had one arrived in Ceylon just in time to see the disappearance of a considerable flora?" To which Bateson promptly responded: "What more likely? Is the alternative interpretation, that he had come in time to attend the birth of a new flora, more acceptable?" (4, p. 42) and he further asked whether Willis really expects the local endemics of the bleak and arid mountain tops to leave those stations and spread over the tropical lowland. It is unlikely that the alpine endemics of Ceylon are really young beginners, and that their case is materially different from that of alpine endemics in many other regions.

In my own studies in eastern America I have found that the unglaciated areas of Newfoundland and Gaspé are characterized by a large flora isolated from the West.

In connection with the occurrence in Gaspé and western Newfoundland of these hundreds of Cordilleran, Alaskan or Siberian species another point of great significance should be noted. This is the very large proportion of strictly endemic species found in these areas. There are more than 80 [after further exploration known to be 100] of these endemic species, plants with fundamental or deep-seated characters in their reproductive organs, all related to plants of British Columbia, Alberta, Washington, California, or Colorado and isolated by distances averaging 2000 miles from their nearest allies. Contrasted with this condition in Gaspé and western Newfoundland the situation in Atlantic western Nova Scotia is illuminating. There, in a region . . . . which was denuded by the Pleistocene glaciers, the flora contains nearly 200 species which, after the receding of the glacial ice, made a landing off the coastal plain which has subsequently become submerged and which now forms the continental shelf or banks off Nova Scotia. These are all plants derived from the southern coastal plain, some of them unknown nearer than the Pine Barrens of New Jersey, one at least unknown nearer than the Carolinas, and nearly all characteristic of the sandy coastal strip from southern New Jersey to Florida and Mississippi, there occurring in a climate obviously much warmer than that of the foggy coast from Digby and Yarmouth Counties to Guysborough, Nova Scotia. Yet in the 25,000 years (more or less) since this flora of far-southern origin became isolated on the Atlantic slope of Nova Scotia it has set off only a single endemic species and that a rapidly reproducing annual, the specific validity of which has been doubted. Otherwise the most Nature has accomplished in Nova Scotia toward segregation

MAP 9. EUROPE IN MID-OLIGOCENE TIME, AFTER GRABAU (40, P. 812.)

from the southern types is the slight increase of hairiness or the modification of stature or foliage in about a dozen species. If we reason that the more thoroughly differentiated species, those with deep-seated differences in flower and fruit, are older than those which show only slight departures from type, then surely the floras of Gaspé and western Newfoundland, with their 80 [now known to be 100] endemic species mostly unrelated to any plants known nearer than about 2000 miles due west, are vastly older than the flora of Atlantic Nova Scotia (33, p. 242).

or Cenozoic time until this propitious moment, when the whole bunch is thrown off at once? In their occupation of very recently disturbed areas, *Rubus* and *Crataegus* are quite comparable with introduced weeds. When Willis's attention was called to the obvious fact that the behavior of the introduced weeds (like the common dandelion, the Canada Thistle, white-weed, burdock, Sheep Sor-

MAP 10. EUROPE IN PLIOCENE TIME, AFTER GRABAU (40, P. 819)

BEHAVIOR IN YOUTHFUL HABITATS

Turning to another angle of the question, if species are "thrown off" in regular mathematical progression through time, as Willis and Yule (93, 94, 95) maintain, how shall we explain the 500–600 (perhaps more) young beginners in *Crataegus* which have sprung up in the last three centuries "on the derelict farms of the Eastern States" (4, p. 42) and adjacent Canada? Have these and the equally modern host of Brambles or Blackberries (*Rubus* § *Eubatus*) simply been accumulating a large credit by withholding their "mutations" since Mesozoic

rel, etc., which in two or three centuries have completely covered the breadth of North America) absolutely disproved Age and Area, in that these are the youngest occupants of a country, not the oldest, he at once altered his definition to exclude introduced plants. But he has not ruled out the New Zealand "Veronicas." In fact, he is very fond of citing them as proof of one point or another in his hypothesis.

Of this group, *Hebe*, in New Zealand Cheeseman says: "*Veronica* presents great difficulties to the systematist. Many of the species are singularly protean . . . . varying so much . . . . that it is no

easy matter to fix their real limits. Intermediate forms are numerous, connecting species that would otherwise appear most distinct, and . . . . these intermediates blend so freely into one another that an apparently continuous series of forms is produced, while several species hybridize so readily in cultivation that the supposition at once arises that natural hybrids may also occur" (16, p. 491). Cockayne, likewise, emphasizes the lack of sharp specific lines in *Hebe* and adds: "Were . . . . that school of botany which is dealing with *Rosa*, *Rubus*, *Hieracium*, and *Crataegus* in the Northern Hemisphere to study the New Zealand forms, several hundreds of species would be forthwith 'created'" (19, p. 44). He might have added *Panicum*, subgenus *Dichanthelium* (the "*dichotomum* group") which multiplies its segregates in the clearings and cranberry bogs of the Tertiary and Quaternary sands of eastern America, *Aster* § *Vulgares* of our swampy clearings and prairies, and many other groups.

Willis repeatedly refers to the fact that, although it is legitimate to consider many groups of endemic or near-endemic occurrence as relics of pre-existing floras "especially in the north temperate zone (particularly North America and China, [see map 6]) where the influence of the last glacial period was severely felt" (91, p. 88), "It would be absurd to apply the 'relic' explanation to such a case as . . . . *Ranunculus* in New Zealand, and yet on this supposition *Ranunculus* in that country, or at any rate *Veronica* [meaning *Hebe*], must be considered as a relic" (91, p. 94). As already pointed out, there is every probability that *Hebe is a relic*, since its range today is almost exactly coincident with the present ranges of such genera as *Nothofagus* and *Araucaria*, both of which are relics of formerly wide-ranging groups. As shown by the statements of ranges in New Zealand given by Cheeseman, 73 per cent of the species of *Hebe* are confined to the South Island (or sometimes to Chatham I. or Stewart I. to the south) and 17 per cent are on both the South and the North Islands; but only 10 per cent are confined to the North Island. In regard to *Ranunculus* Cheeseman states: "In New Zealand it forms a very conspicuous portion of the mountain vegetation, especially in the South Island . . . . Many of them are exceedingly variable and difficult of discrimination. . . . . Of the 37 species known, ... 31 are endemic" (16, p. 7); and it is notable that the "difficult" species are exclusively among the endemics.

Now, so far as I can see *Hebe* and *Ranunculus* in New Zealand are misbehaving, like *Crataegus*, *Rubus* § *Eubatus*, *Hieracium*, the dichotomous Panicums, and numerous other groups in the northern hemisphere, for the simple reason that these groups, often of ancient lineage, have suddenly had opened before them large areas of virgin territory ready for invasion, and in the rapid occupation of the new habitats the formerly isolated and well-behaved species have freely mingled, with the result that we now have an intricate maze of undifferentiated and freely intergradient plants. In fact, Bateson has already stated that, "No one familiar with genetical work would be disinclined to believe that the vast group of endemic shrubby Veronicas were co-derivatives from one or more crosses" (4, p. 42). This interpretation in *Rubus*, *Rosa*, *Crataegus*, etc. is familiar. That the South Island of New Zealand was severely and recently glaciated there can be no question. Here are the words of Geikie: "the existing glaciers of New Zealand are the descendents, so to speak, of far greater ice-flows, which reached the

plains . . . . and may even have entered the sea. . . . . The positions occupied by the terminal moraines . . . . show that the old glaciers were of very considerable importance . . . . after these moraines were deposited, the glaciers appear to have retreated continuously, and perhaps somewhat rapidly, as no terminal moraines are again met with, except in the immediate neighbourhood of the existing ice-streams. . . . . In the south island of New Zealand . . . . we find a close analogy to the conditions that obtain in Scandinavia and Scotland" (37, pp. 717–719). It is, therefore, highly significant to find that ancient *Ranunculus* and presumably ancient *Hebe* have revived their youth and are now multiplying their species on the recently glaciated area of southern New Zealand, just as the ancient genera, *Rubus*, *Crataegus*, etc. are doing in the most youthful soils of the northern hemisphere. How can Age and Area tell us that *Rubus*, *Crataegus*, *Quercus*, *Ranunculus* and many other rejuvenated genera (probably including *Hebe*) are as old as *Liriodendron*, *Sassafras* and *Hamamelis*? Yet they are undoubtedly quite as old. This simple fact, that some of the Mesozoic genera are now seemingly on the wane while others of equal antiquity have revived their youthful vigor and pioneering capacity, is sufficient wholly to discredit the notion that we can determine the age of a group merely by the area it covers or by the number of its species.

RANGES OF ENDEMICS

The endemics just discussed are obviously very young indeed and except that Willis, himself, draws them into the discussion by emphasizing *Hebe* and the New Zealand species of *Ranunculus*, they might be ruled out, not only because they act like the introduced weeds, but because Willis claims that he restricts his discussion to "Linnean species." In general, alpine endemics are of the latter class and in discussing these epibiotics of Eurasia and Willis's view that they are young beginners, Ridley says: "I do not clearly see why . . . . the Alpine plants of the high mountains of the Malay Peninsula and Ceylon have a tendency to the reduction of leaves, and their having a tendency to become eventually quite round, orbicular in fact, and in case of compound leaves, simple, a state of affairs which does not occur in any of the species of the same genus in the wet forests at the base of the mountains; but there cannot be a shadow of doubt that it is of importance to the plant, and that the plants have been gradually adapted to their surroundings" (65, p. 565). And after discussing other cases in Ceylon and showing that Willis does not know the plants and their habitats but simply makes mechanical compilations, Ridley continues: "I confess I do not understand Dr. Willis's interpretation of the simple facts of evolution of a species as generally understood by naturalists. He states that the idea that endemic species were evolved to suit local conditions is based largely upon Wallace. Who ever possessed such a curious idea? Let us take some examples of endemics. *Aphyllanthus monspeliensis* is a liliaceous plant occurring in a limited area on the Mediterranean where it is distinctly endemic, a monotypic genus of the Sowerbieae section with no relations nearer than Australia. *Helxine Solerolii*, Req. (Urticaceae), is an endemic of Corsica and Sardinia and has no relations at all in this region. *Dioscorea pyrenaica*, Bub., is endemic to the Pyrenees and the only species of its genus in Europe. How could these plants be evolved to suit local conditions, unless they are the relics of floras of which the rest is extinct? There is nothing within

thousands of miles of them now from which they could be evolved. In cases like this, and there are very many, his mutation theory utterly collapses" (65, pp. 568, 569).

Willis's rhetorical query, in regard to the endemics of the Ceylonese mountains has been noted. In that case the plants were obviously relics. He makes a similar query in regard to *Senecio*. "It is very hard to suppose that a genus would choose certain spots upon the globe where its species should die out in large numbers, yet the facts of distribution require that this should be so under this explanation. Why should the *Senecios* retire to die, in large numbers, to Mexico, California, Bolivia, Peru, South Africa, Australia, etc.?" (91, p. 89). Who but Willis ever suggested that *Senecio* as a genus is dying out? As we have seen, following Small, he originates the genus in the northern Andes many millions of years before the high Andes of today existed. There the genus has phenomenal development and is a *mature* rather than a *dying* group. The monographer of the group, Greenman, finds that "There has been a relatively rapid northward migration of species . . . . as far north as east-central Mexico and Cuba;" that there is "greater stability in morphological characters of the species occupying large areas as compared with the species occupying small areas—thus according in general with the age-and-area hypothesis;" but that "The origin of the respective species in the groups of plants specially considered appears *not* to have been through mutation of large size only, as held by Willis for the 'endemics' of Ceylon and New Zealand, but rather through natural selection in the course of a relatively rapid northward migration" (41, p. 193). In other words, *Senecio* in the mountains of tropical America has not "retired to die" but is in the most active stage of maturity, not, as Small and Willis think, because it originated in the Cretaceous but because it is in a region geologically young. In the Andes and Mexico it is doing exactly what *Hieracium*, *Centaurea*, *Dianthus*, *Astragalus*, *Artemisia*, *Eriogonum*, *Hebe* and numberless other overwhelmingly large genera are doing in relatively youthful country in other parts of the world, certainly not "retiring to die."

Again Willis says: "The comparative rarity of seriously broken areas of distribution among endemic forms, especially south of the influence of the last glacial period, is much against any very large amount of dying out. One would not expect a moribund species to retain its area intact—though it is true that with the Cycads, often supposed moribund, this is largely the case" (91, p. 89). The Cycads are certainly more than "supposed moribund;" but, in regard to the general proposition, it is difficult to visualize a plant or animal having "seriously broken areas of distribution" and at the same time being "endemic;" and, in view of the recent glaciation of southern South America, southeastern Australia and Tasmania and southern New Zealand, it is likewise difficult to visualize any extensive flora and fauna "south of the influence of the last glacial period." Since Willis repeatedly states that, although Age and Area may break down in the North, but is the general rule in the region "south of the influence of the last glacial period," we are inclined to agree that it may be; the flora and fauna of the Antarctic ice-field may follow it! As to the "endemics" with "seriously broken areas of distribution," it may be possible that Willis is here adopting his recent redefinition of an endemic: "On larger areas of ground the proportions are

greater; Brazil has about 21 per cent of its genera endemic, and so has Chile, Australia about 30 per cent, ... and the proportions increase with increasing area till one finds 100 per cent endemic in the World" (**91**, p. 170). In this larger area, where 100 per cent of the plants and animals occur (assuming that there are none in other worlds), there are so many groups (families, genera or species) with "seriously broken areas of distribution" that their detailed enumeration would nearly occupy the space of this article. Sufficient illustrations of them have already been given.

DISPERSAL OF SPECIES NOT CENTRIFUGAL

In regard to Willis's idea that plants originate at a center and then spread like concentric rings, it is obvious that he is dealing again with his imaginary world. Many botanists, Mrs. Arber, Sinnott and others, have discussed the theoretical objections and Schonland says: "the crux of Willis's 'Age and Area theory' consists in the assumption, that the dispersal of a species and of the new species derived from it must be centrifugal. Theoretically this may be conceded at the start, but by no means for all time to come" (**68**, p. 469). And Rendle remarks: "we cannot but hope that after all this is not the conclusion of the whole matter. If species originate by mutation and evolution and distribution are purely mechanical processes, what more is to be done?" (**64**, p. 307). This idea, that plants, after they have once got a start, *radiate* from a center, although erroneous, is common. For instance, such an idea in regard to our Arbor Vitae or White Cedar, *Thuja occidentalis*, whose ancestors date back to the Mesozoic, was recently put forward. Of this notion I wrote: "Hutchinson says . . . . 'The northern area of its distribution is roughly outlined by a semicircle, a fact which contributes evidence that *Thuja* has migrated radiately from a limited area . . . . it does not migrate rapidly . . . . this form has lagged behind.' When, therefore, following Hutchinson's suggestion, we draw the circle connecting the 'outliers' . . . . it is impressive to find that the center of the circle falls in the great acid Archaean area northeast of Lake Superior, the Temagami region; for Hutchinson particularly informs us that 'it is notable that throughout great areas, for instance the Temagami region, *Thuja* is unknown.' And since the Temagami region was not accessible to forests until the vanishing of the Pleistocene ice, by Hutchinson's interpretation that the tree has 'migrated radiately' we are forced to the dramatic picture of the infant *Thuja occidentalis* created in very modern times in the center of the Temagami region and finding nothing to live on, migrating as rapidly as its 'lagging' tendency would allow to the calcareous regions northwest, north, east and south!" (**30**, p. 64).

Surely every botanist with the slightest experience in the field knows that in general plants do not spread radiately over large geographic areas. They follow belts of special soils, humidity or temperature and, with a great diversity of individual ecological or physiological requirements, each works out its range, which is anything but mathematically regular. Plants and animals in their dispersal are opportunists; their ranges are essentially all different and cannot be reduced to simple geometric patterns.

LIGNEOUS AND HERBACEOUS ALLIES

With *Hebe* of New Zealand still in mind let us look at Willis's reasoning about it (as "*Veronica*" in New Zealand). Arguing that ligneous groups are in general older than herbs, he says: "Only

very rarely, again, will one find a group of ten allied herbs, with a group of ten allied trees closely related to it. In such a case, which will very seldom occur, comparisons on the basis of age will be impossible" (91, p. 86); and again, "No one would suggest that a herbaceous genus of 100 species was of the same age as a tree genus with 100" (91, p. 116). Surely, *Hebe* (which, as we have seen, Cockayne believes to have hundreds of species equivalent in degree of segregation with those of *Crataegus*, *Rubus* and *Hieracium*) is closely related to the herbaceous genus *Veronica* (or the subgenus *Euveronica*). It consists of shrubs and trees and certainly Willis, by inference at least, derives them from the herbaceous genus of the northern hemisphere: "great ranges of mountains have sprung up . . . . it is clear that they have completely altered the distribution of species . . . . though on the other hand, species, chiefly herbaceous, which can live at high levels in the mountains, have been enabled to travel through and into regions otherwise impassable. It is in this way, probably, that many herbaceous and shrubby types of vegetation, including . . . . *Veronica*, characteristic of the north temperate regions, but now also found in New Zealand, South America, etc., have been enabled to reach these countries" (91, p. 40). Willis merely infers the derivation of *Hebe* from the herbaceous Veronicas, but Cockayne gets beyond inference, saying in his paper, *Evolution of the Genus Veronica in New Zealand* (19, p. 44): "There is every evidence, then, of descent from a common ancestor, which, considering the genus beyond New Zealand as well as within its confines, would probably be an herbaceous plant with a didynamous capsule, such as *V. Chamaedrys* L." As I have already indicated, however, Pennell finds good reason to consider *Hebe* more primitive than *Veronica*. This does not necessarily mean that all living woody genera, subgenera and species are older than their herbaceous allies. We know too many herbaceous types which are presumably of Mesozoic origin to believe that; and in the youthful flora of the cordilleran region of tropical America (mostly of Pliocene, Pleistocene or later origin) there are many ligneous members of groups which in older floras are represented only by herbs. The Morning Glories, *Ipomaea*, for instance, in the ancient floras of Australia and South Africa are herbaceous or at most suffruticose or woody climbers, but in the region from western Mexico to Peru there occur numerous large trees (*Ipomaea* § *Arborescentes*); or *Oxalis*, which in South Africa is a large genus of geophilous herbs, in the youthful region from Mexico into the Andes has many ligneous representatives.

THE "HOLLOW CURVE"

One other point remains to be considered: Willis's "hollow curve." This Willis lays great stress upon, but the very definite fact, that competent mathematicians differ radically in their evaluation of it, is sufficient indication that, until its status is cleared, it is not an implement for the average botanist or zoölogist who deals with thousands of organisms, each with an independent life-history and geographic range. Willis, vigorously supported by Yule, finds the "hollow curve" the one correct representation of the facts of dispersal and evolution, but many others who have investigated it find it useless. Regan's flat statement that Age and Area "has no value" was based on a study of the "hollow curve" in which he showed that the same curve could be derived from a tabulation of the "names in a directory according to the

number of times each appears, etc., etc. . . . . In other words the curve is not due to a single factor" (62, p. 165). Pantin, by making legitimate assumptions different from those of Willis, "came to conclusions directly opposite to those of Dr. Willis" and found that "we have in his curves direct evidence that:—(1) Evolution has proceeded almost entirely by natural selection . . . . (2) . . . . it is impossible to conceive of evolution proceeding by the large mutations suggested by Dr. Willis" (58). Newton, likewise, taking the same data as Willis, concluded: "It is now possible to deduce the converse of Dr. Willis's theorem" (57); and Chamberlain, after many tests of the work of "lumpers" and of "splitters" and with the crudest work and the best of monographs, concluded that "only in the most general sense will the quality of the data effect the form of the curve" (14, p. 308). With the mathematicians in complete disagreement as to the value of the "hollow curve" as a measure of evolution, the student of distribution can safely let it alone.

CONCLUSION

In this study I have purposely omitted any detailed discussion of the method of origin of species, since we are dealing with the dispersal not the origin of the organisms. I have also been obliged to omit practically all reference to the standpoint of the morphologist, the genetecist and the ecologist, since, with limited time for preparation, it has been necessary to keep pretty closely to the fields of classification and geographic distribution, which are most intimately concerned. In such discussions by the morphologist, genetecist and ecologist as I have come across there is no indication of approval of Age and Area; and, except for the applause of de Vries, the subject has produced hardly a ripple in Europe south of the English Channel. Only the mathematicians and the philosophers see value in it and that is natural enough. It is an attractive concept and to those who do not realize the gross errors of fact involved, it seems very reasonable. Its only generally accepted proposition, however, is a truism which is not new. If the world were static it would be the obvious law. The world not being static, life has followed an intricate and almost inextricable series of factors, each acting differently on different species, with the result that no single factor, and especially *age*, can be isolated as all-controlling. Willis, as I have tried to show, has proceeded "without a full appreciation of the axiomatic truth that a work on phytogeography should be based on a clear understanding of identities and of the geographic ranges of plants" (29, p. 215). "There is no branch of the botanical field which so much as phytogeography demands thorough training in exact taxonomic detail accompanied by the most discriminating judgment and prolonged and painstaking field-study" (29, p. 214); these Dr. Willis too obviously lacks. He has reared a superstructure with many attractive features but, unfortunately, he has neglected to consult frequently enough the taxonomists, the "hodmen of science" (see 52) and their co-workers in paleontology, geology, morphology and ecology, who control the brick and mortar necessary for the foundation. Without the secure foundation, which they in coöperation have to supply, the superstructure must necessarily collapse. "Age and Area" in 1915 was a "law;" by 1917 it had become "a hypothesis" and on the last page of his book, in 1922, Willis stated that it was "simply a corollary." By the mathematical rule which Willis believes to control all evolution, its status in 1926 could readily have been foretold.

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This bibliography, concerning so large a field, does not profess to be complete, and from the necessity of preparing this paper during a short vacation I have been forced to restrict it largely to the immediate fields of systematic and geographic botany and I have scarcely entered the fields of paleontology, morphology, ecology, genetics, etc., in their relation to Age and Area. It has seemed unnecessary to repeat most of the references published by Willis, but rather to supplement his bibliography.

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HOST RESISTANCE AND TYPES OF INFECTIONS IN TRYPANOSOMIASIS AND MALARIA

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I. INTRODUCTION

CLASSICAL immunology has been chiefly concerned in the past with the host and not the parasite. It has attempted to study the properties of immune sera as opposed to normal sera and to correlate the former with the defense of the host against the invading parasite or to use the former in detecting the presence of a suspected parasite. In the present review the author wishes to shift this emphasis slightly by correlating the properties of immune sera with the activities of the parasite. By this approach to the subject it is hoped that some of the immunological bases for the different types of infection will be disclosed.

The difficulty of studying the subject from this aspect lies in the fact that in order to get at the activities of the parasite all the stages in its life-cycle must be localized in some accessible part of the host where they may be studied from day to day. Certain of the plasmodia and trypanosomes comply with this prerequisite since they complete their life-cycle in the general blood stream and can be found in the peripheral blood. They will, consequently, be taken up in detail, while others, unsuitable in this respect, will not be considered. Thus, *Trypanosoma cruzi*, which shows more similarities to the leishmanias than to the trypanosomes, is predominantly a tissue parasite and can only rarely be found in the blood-stream. Likewise, *Halteridium* of birds and *Plasmodium falciparum* of man undergo their asexual life-cycles chiefly in the blood vessels of the deeper tissues.

For a detailed description of the parasites considered in this review and their relatives, the reader is referred to any of the standard texts on protozoology, such as Hegner and Taliaferro (1924). Only the barest details can be given here. The genus *Trypanosoma* is very widely distributed, and species are found parasitic in the blood of various vertebrates belonging to almost every class. In the present paper a distinction is made between pathogenic and non-pathogenic or non-lethal forms. By far the majority of the known species belong to the second group and produce no observable symptoms in their hosts. A representative of this group is *T. lewisi*, the common blood parasite of rats all over the world. By pathogenic trypanosomes is generally meant those which produce disease in man or animals, such as, *T. gambiense* and *T. rhodesiense* of human sleeping sickness, *T. cruzi* of Chagas' disease, *T. brucei* of nagana of domestic animals, *T. equinum* of mal de caderas of horses and mules, and *T. equiperdum* of equine dourine. Even these forms which are generally lethal to man or domestic animals can probably live in certain wild animals without producing appreciable symp-

toms. Among the malarial parasites, *Plasmodium falciparum*, *P. malariae* and *P. vivax* of the malignant tertian, quartan and benign tertian fevers of man are too well-known to need discussion. In man, malaria, though often fatal, tends toward recovery. *P. relictum*, the bird parasite, is generally non-lethal.

Figure 1 gives some outline drawings of *Trypanosoma lewisi* taken (1) when the parasites are actively reproducing, (2) when actual cell division is rare, but when growth stages due to reproduction are still present and (3) when all reproduction has stopped. Although the pathogenic trypanosomes considered do not reach a stage, in laboratory animals, when all cell division ceases, their morphology differs from *T. lewisi* only in minor details. Figure 2 shows the intracellular bird malaria parasite (*Plasmodium relictum*) and indicates the 24-hour asexual cycle which occurs in this parasite.

A knowledge of the general course of infection of the trypanosomes and malarial organisms has gradually accumulated as a result of many types of experimental work. The author cannot, therefore, review progressively the steps in its compilation, but will, instead, outline the general facts in regard to these infections, and in passing, note a few specific pieces of work which seem particularly important. Moreover, to avoid repetition it has seemed best, first, to outline briefly the methods devised for determining the effects of the host's resistance on the parasite in the various types of infection, and second, to follow this with a consideration of each of the main types of trypanosome and malarial infections. These types of infections will in turn be discussed with regard to the following points: first, to review the course of the infection; second, to apply the methods of analyzing the effects of resistance which will have been previously outlined; and third, to give the immunological bases for these effects in as far as they are known.

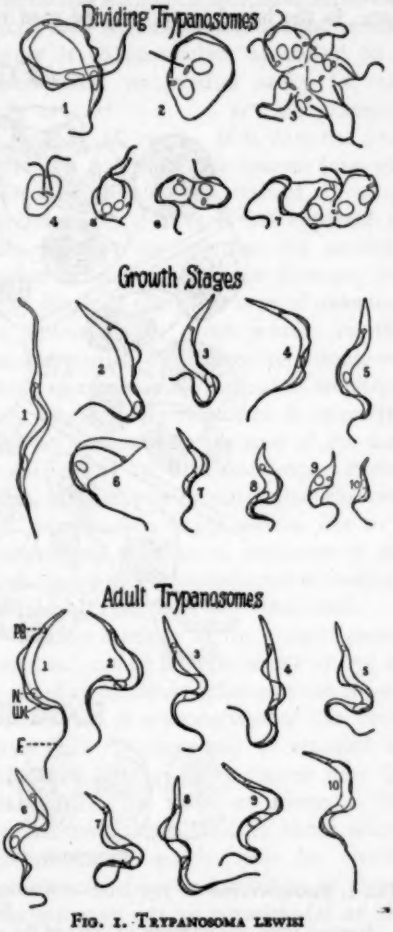

FIG. 1. TRYPANOSOMA LEWISI

1. Dividing trypanosomes such as are found at the height of reproductive activity. 2. Growth stages, taken from the fourth day of the infection shown in figure 3. 3. Adult forms, taken from the twenty-eighth day of the same infection. *F*, flagellum; *N*, nucleus, *P. B.*, parabasal body; *U. M.*, undulating membrane. × 1000. (1, after Coventry; 2 and 3, after W. H. Taliaferro.)

Before taking up the methods devised for determining the effects of the host's resistance on the parasite, the term resistance, itself, needs defining. Resistance, in the broad sense, may be used to denote various mechanisms, either active or passive, of the host to counteract the activities of the invading parasite. It may be manifested as hindrances to the act of invasion; as conditions arising in the body of the host adverse to the parasite; as efforts on the part of the body to make good the deleterious effects of the parasite as in the hyperactivity of the hematopoietic organs due to the destruction of red cells in malaria; or by the production of antitoxins in those infections where toxins are formed. Throughout this paper, however, the term resistance will be restricted, as a matter of con-

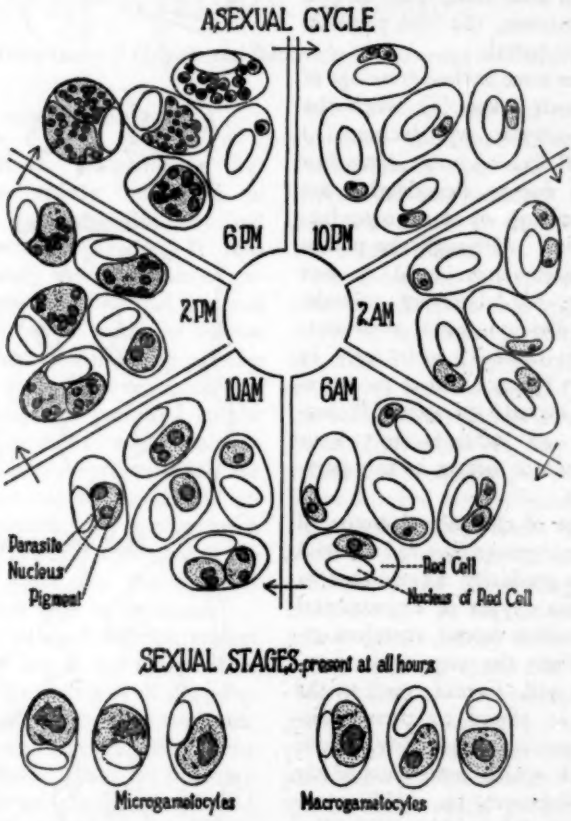

FIG. 2. REPRESENTATION OF THE CYCLE OF REPRODUCTION IN BIRD MALARIA SHOWING CHANGES IN SIZE AND VARIABILITY

Outlines of the asexual stages (×1500) of the parasites within the red cells, showing nuclei and pigment granules, made at four hour intervals during a consecutive period of 24 hours. In addition, outlines of three microgametocytes and three macrogametocytes, which occur in small numbers at all hours throughout the infection. (From drawings by L. G. Taliaferro.)

venience, to denote the various conditions arising in the host which are adverse to the parasite, since the author hopes to show later that the different types of infection may be directly correlated with the host's resistance in this sense. It is also to be noted that resistance in any sense may be either natural or acquired. Natural resistance is correlated with such matters as species immunity, etc., and although it undoubtedly plays some part in the types of infection, it may not be the result of infection. Acquired resistance, on the other hand, is developed after the parasite has successfully invaded the host, and, as will be shown later, is adequate to explain the broad differences in the various types of infection considered in this paper. The present review, therefore, will be limited to considerations of acquired resistance.

Acquired resistance, as just defined, is generally thought of as paralleling the production of immune antibodies or reaction products in the host. "As antibodies have never been isolated in a pure condition we have no knowledge as to what they are, and their existence is recognized merely by the effects they produce, just as we recognize the existence of enzymes" (Wells, 1925). Furthermore, although they may represent new material substances arising in the host as a result of infection or processes of immunization, they may just as well represent a change in substances already present or even a change in substances already present or even a change in the concentration of such substances.

II. METHODS OF ANALYZING THE EFFECTS OF RESISTANCE

The methods devised for determining the effects of the host's resistance on the parasite in the various types of infection can now be outlined. Granted that a parasite not only has successfully invaded its specific host but has started reproduction, it is evident that if no resistance is operative it must increase in the blood at a uniform rate. Also, due to the fission-method of protozoan reproduction, such an unmolested increase would cause it to accumulate according to a geometrical progression series (a, ar, ar^2, ar^3, ar^4 . . . . . , ar^n, for example, 1, 2, 4, 8, 16, etc.). If it does not progress uniformly in this manner (and the majority of infections studied do not), for example, if after it has appeared in the host as an infection, its numbers either remain constant or decrease, we may conclude that some type of resistance is operative. In other words, in the number curves of different infections, we have an approximate method of ascertaining whether any resistance is operative and an approximate measure of the sum total effects of this resistance. Parenthetically, it may be noted that the rate of reproduction might *increase* due to a lowering of the natural resistance of the host, but with little experimental evidence indicating this, it is not considered.

Any fluctuations in the number curve, however, can be brought about by one or both of two entirely different mechanisms: 1, the rate of reproduction of the parasites (cell division) may be retarded or inhibited; or 2, the parasites may be destroyed after they are formed. The second mechanism includes those effects of resistance which may be termed *parasiticidal*, but the inhibition of reproduction may not be parasiticidal at all. Practically all discussions of the effects of resistance have hitherto been limited to the parasiticidal effects.

Although the general phenomenon of the cessation of reproduction in infections with *Trypanosoma lewisi* has been known for many years and the presence of cycles of reproduction in *T. gambiense*

since 1912 (Robertson, 1912), the sharp distinction between these two effects of resistance was probably first clearly brought out by the present author and L. G. Taliaferro (1922). The principle of inhibition of reproduction as an immune phenomenon is recognized by van Saceghem (1923) and definitely correllated with a property of immune serum by Taliaferro (1924). These investigations will later be considered in detail. As Taliaferro, W. H. and L. G. (1922) point out, the separate action of the reproduction inhibiting and the parasiticidal effects of resistance which collectively account for the number of organisms present in the blood at any time is clearly indicated in the following equation:

$$\left.\begin{array}{c}(1)\\ \text{Number of parasites at any time}\end{array}\right\} = \left\{\begin{array}{c}(2)\\ \text{Number produced by reproduction}\end{array}\right\} - \left\{\begin{array}{c}(3)\\ \text{Number destroyed}\end{array}\right.$$

Here the reproduction inhibiting effect directly affects the second member of the equation and the parasiticidal effect represents the third member. As the members of this equation can not be measured exactly it can not be solved in a mathematical sense. Nevertheless, fairly accurate conclusions can be drawn by the methods outlined in the next paragraphs.

In the work of Taliaferro, W. H. and L. G. (1922) and Taliaferro, W. H. (1924) on trypanosomes, and Taliaferro, L. G. (1925) on bird malaria, the first and second members of the equation have been determined and the third evaluated in the following manner. The first term can be easily obtained by making frequent parasite counts during the course of an infection. The second term of the equation (rate of reproduction), in order to be valid, must be independent of both the first and third terms, and hence, can in no way depend on the enumeration of the progeny formed. A measure to fill these requirements has been found and although it is indirect, it can be used as long as there are enough parasites in the blood to furnish suitable samples for analysis. Since reproduction in malaria, however, proceeds in cycles, whereas in trypanosome infections it does not, a different method is used in the two groups.

In the trypanosome infections, the measure consists, essentially, in comparing the variability in size of samples of trypanosomes taken at stated intervals throughout the course of an infection. The rationale of this method is based on the obvious and well-known fact that a sample of organisms measured, on the one hand, from a population undergoing rapid reproduction, with the constant production of young forms and intermediate growth stages, will exhibit much greater variability in size than a sample of organisms measured, on the other hand, from a population in which there is little or no reproduction and in which all of the organisms are full-grown adults. (Compare, for example, the variations in length of the reproducing with the constancy in length of the non-reproducing parasites in figure 1.) Throughout the work, the total length of the trypanosomes was selected as the most suitable measure of size while their variability was expressed in terms of the coefficient of variation. This statistical constant was computed from the actual measurements by means of the usual formula and expresses the variability in terms of percentages of the mean size. In *T. lewisi*, for example, a coefficient of variation for total length of 3 per cent indicates a population of adults in which there is no reproduction and a coefficient of variation of 30 per cent indicates a population in

which reproduction is ensuing at a maximum rate.

The coefficient of variation method is applicable to trypanosome infections because in these the organisms reproduce by binary fission and do not exhibit any periodicity in reproduction. Thus, if reproduction is going on, a random sample at any time will give all stages of reproduction and growth. In the malarial parasites, however, the asexual forms sporulate and grow up nearly synchronously (cf. fig. 2). Thus, a sample at one time will contain only small forms (merozoites); at another, large forms (schizonts), etc. The length of time it takes for the organisms to complete this cycle of growth and sporulation is the time it takes for each small organism to grow up and produce about 15 progeny, and is, therefore, actually an expression of the rate of reproduction of parasites. Should this time vary anywhere during the infection, the rate of reproduction could accordingly be said to vary. It is to be noted that examinations of blood smears to ascertain when sporulation takes place would give a rough measure of the rate of reproduction. A more exact method, which was the one used, is as follows: 50 parasites were drawn, measured and their mean size obtained at 2- or 4-hour intervals during as much of the infection as was possible. As can be seen from figure 2, the data obtained showed a series of abrupt falls and gradual rises in the mean size of the parasites, due to the fact that when the parasites occurred in the blood as large schizonts, their mean size was high; when sporulation took place, their mean size immediately dropped, but gradually rose, as growth ensued, until the next period of sporulation. Comparing the time it takes for this cycle to be completed during the various stages of the infection (acute, chronic and relapse) it can be ascertained whether the rate of reproduction is changing or being maintained constant. In one strain of bird malaria, for example, the cycle was found to take twenty-four hours whenever it was possible to obtain data, and therefore, the rate of reproduction can be considered as constant throughout the entire infection. This measure of the rate of reproduction supposes that the *average* number of young produced by each full-grown parasite at each sporulation period does not vary throughout the infection. This has been shown to be a valid assumption by L. G. Taliaferro (1925). Obviously, this method has the same advantage as the coefficient of variation method in the trypanosome infections in that it is independent of the number of parasites destroyed, and can be used as long as enough parasites remain in the blood to obtain a statistically valid sample.

III. CONTINUOUS INFECTIONS OF THE PATHOGENIC TRYPANOSOMES IN THE MOUSE

When most varieties of the pathogenic trypanosomes which produce disease in man and domestic animals are injected into mice, the parasites appear in the blood after a short incubation period and increase in numbers steadily and uniformly until the death of the host. This is the simplest type of infection met with. Much the same type of infection is seen in the rat. Sometimes, however, the parasites in this host temporarily disappear from the blood and the infection, consequently, more nearly approaches that seen when the pathogenic trypanosomes are grown in the guinea pig as described in the next section. The general nature of the infection in the mouse and its difference from that in the guinea pig was recognized by the earlier writers; for

example, it was clearly pointed out by Massaglia (1907).

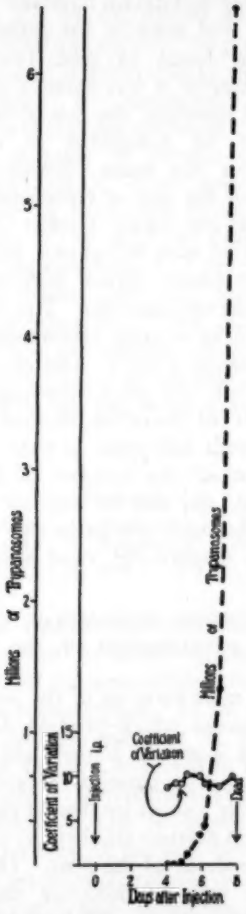

FIG. 3. GRAPH SHOWING THE COEFFICIENT OF VARIATION FOR TOTAL LENGTH (COMPARATIVE MEASURE OF THE RATE OF REPRODUCTION) AND THE NUMBER OF TRYPANOSOMES PER CUBIC MILLIMETER OF BLOOD, THROUGHOUT THE COURSE OF AN INFECTION WITH T. RHODESIENSE IN A MOUSE

This infection illustrates the condition in which there is neither any inhibition of reproduction of the parasites nor any appreciable parasiticidal action. (From data by W. H. and L. G. Taliaferro.)

T. rhodesiense, the causative agent of one type of human sleeping sickness, in the mouse, taken from Taliaferro, W. H. and L. G. (1922), illustrates this type of infection. After an intraperitoneal injection of infected blood, the trypanosomes appeared in the blood 4 days later, and the mouse died 7 days after injection. (See fig. 3.) Blood smears were made every 12 hours while the organisms were in the blood. After staining and upon examination, they gave the results which are represented graphically in figure 3. (In the graphs of the trypanosome infections, i.e., figures 3, 4, 5, and 6, all of the data are represented on the same scale with the exception of the number curve in figure 3 which of necessity is considerably reduced. This makes possible a direct comparison of the different types of infection.) The variability of the parasites remained fairly high (C.V. = 8.87 to 10.46 per cent) throughout the infection with no indication of a progressive change in it—from which we may conclude that the rate of reproduction remained approximately the same throughout. Furthermore, microscopical examination of the slides showed that cell division of the parasites was occurring throughout the infection. The number of organisms in the blood steadily accumulated according to a geometrical progression which, as has been said before, is just what would be expected if none or very few of the organisms were being killed. Hence, we may conclude that no resistance whatever is acquired by the host, either affecting the rate of reproduction of the parasites or destroying them after they are formed.

IV. INFECTIONS WITH PATHOGENIC TRYPANOSOMES PROCEEDING BY CRISES AND RELAPSES

When the same pathogenic trypanosomes considered in Section III are grown in the guinea pig, the infection is charac-

terized by alternate increases and decreases in the number of parasites found in the blood (fig. 4). The periods of more or less sudden disappearance of the parasites from the blood are known as crises and the re-population of the blood following the crises as relapses. As has already been pointed out, the general nature of such infections has been well-known for a number of years. Fantham and Thomson (1911) applied exact enumerative methods throughout the course of infections of *T. rhodesiense* and *T. gambiense* in guinea pigs and rats, and Thomson (1912) has applied the same

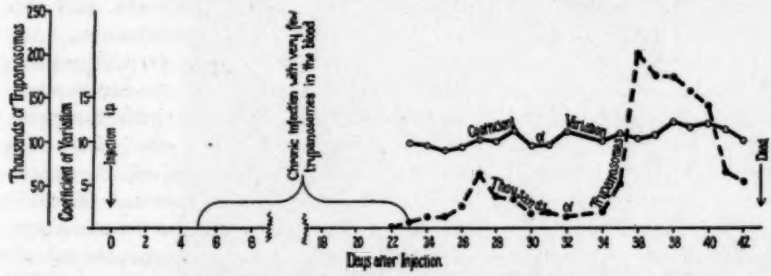

FIG. 4. GRAPH SHOWING THE COEFFICIENT OF VARIATION FOR TOTAL LENGTH (COMPARATIVE MEASURE OF THE RATE OF REPRODUCTION) AND THE NUMBER OF TRYPANOSOMES PER CUBIC MILLIMETER OF BLOOD, THROUGHOUT THE COURSE OF AN INFECTION WITH T. RHODESIENSE IN A GUINEA PIG

This infection illustrates the condition in which there is no inhibition of reproduction of the parasites, but in which there is a marked parasiticidal effect, as is shown by the first chronic stage of the infection and by the two well-marked number crises. (From data by W. H. and L. G. Taliaferro.)

methods to infections with *T. brucei* in the same hosts.

Besides the guinea pig, this kind of infection has been found in other hosts. Thus, it is quite often observed when the dog is infected with the pathogenic trypanosomes; it was found by Ross and Thomson (1910*a*) to be characteristic of infections of *T. rhodesiense* in man, and in the author's experience, generally occurs when *T. equinum* is grown in rats.

The sudden disappearance of the parasites from the blood, coupled with the *in vitro* serological studies which we will review later, early convinced investigators that the crises were actual periods of wholesale destruction of the parasites and not simply periods of temporary migration of the organisms from the blood stream. In analyzing the effects of the host's resistance to the organisms, therefore, it may be concluded from this early work that one effect of resistance in these infections is the destruction of large numbers of the parasites at certain intervals. Is this destruction associated with any effect on the rate of reproduction *per se*? Our work indicates that it is not. For example, the coefficient of variation for total length (Taliaferro, W. H. and L. G., 1922) of *T. rhodesiense* throughout an entire infection in the guinea pig remains at the high level of 9 to 10 per cent (fig. 4). Essentially similar results are obtained in the dog. Here, as in the infections in the mice, direct microscopical examination of the slides showed that the parasites were undergoing cell division whenever they could be found. In other words, once the parasites are introduced into the host, they probably reproduce at a uniform rate during the entire infection. At intervals, however, most of the parasites that have accumulated in the blood are destroyed, but the few, which escape destruction, since their rate of reproduction is unchanged, repopulate

the blood again and again until the host dies. Expressed in terms of resistance, in this type of infection, which proceeds by crises and relapses, one of the two possible effects of resistance is operative, i.e., the host's resistance is directed toward a destruction of the parasites after they are formed but not toward an inhibition of the rate of reproduction *per se*.

What is the mechanism of this destruction? The available evidence indicates that at the crisis there is a sudden acquisition of a trypanolytic property by the blood serum and that the organisms accumulate in the blood during the relapse *not* because the lytic antibody disappears but because the trypanosomes are so changed biologically as to be no longer susceptible to the action of the antibody. These data have been obtained from two different lines of investigation: first, the study of the trypanocidal antibodies arising in animals as a result of the partial or complete cure of infections, and second, the study of the trypanolytic antibodies occurring during the uninfluenced course of experimental infections. Although it might be questioned whether the trypanocidal effects in these two classes of experiments are the same, they nevertheless point to the same conclusions.

It was recognized early in the experimental work with trypanosomiasis that the serum of some infected animals lysed the same species of trypanosome. This phenomenon was probably first noted by Schilling (1902) in a bull "immunized" against nagana (*T. togolense*). Franke (1905) also noted it in an Old World monkey (Cercopithecidae) cured of mal de caderas (*T. equinum*). He also observed the very important fact, from the standpoint of the mechanism of relapse, that the blood of the infected monkey could contain simultaneously the trypanosomes and strong trypanocidal antibodies. Evidently, these resistant organisms were different from the original passage strain, and he states, "dass die Parasiten andere biologische Eigenschaften angenommen haben und für die Schutzstoffe unempfindlich geworden sind." Lingard (1904) also noted that the serous fluid from the plaques of horses with dourine (*T. equiperdum*) was trypanolytic.

The study of the trypanocidal antibodies which arise following treatment and their relation to relapse antedates the work on the course of natural infections and will therefore be considered first. Beginning with the original work of Franke (1905), Ehrlich and his coworkers, Roehl, Gulbransen and Ritz, have carried out a very ingenious series of experiments on the mechanism of relapse in infections with the pathogenic trypanosomes in the mouse. As has already been pointed out, the uninfluenced infection in this host is of the continuous progressive type, and therefore, crises and relapses had to be produced by means of incomplete cures with drugs. With such artificially produced crises and relapses, they tested the identity or non-identity of their original and relapse strains by using a previous observation of Ehrlich and Shiga (1904), which was confirmed by Halberstaedter (1905) and Franke (1905), that if a mouse is cured of an infection with a pathogenic trypanosome, it is refractory for about 20 days to a second infection with the same strain. This immunity is so specific that it serves to differentiate between the original and the relapse strains. In this type of work it might be thought that the immunity after cure is due to the retention of the trypanocidal drug. Ehrlich and Shiga (1904) showed that this was not true but that it is connected with a specific immunological reaction on the part of the host. It has also been shown that par-

tial cure results in the production of similar specific antibodies.

An hypothetical experiment will serve to show how these experimenters differentiated original and relapse strains: A mouse is infected with a strain of trypanosomes which is called the *passage* or original strain. When the trypanosomes appear in the blood, a trypanocidal drug is given to the mouse in a dose sufficient to cause a temporary but not a permanent disappearance of the parasites from the blood. The parasites which reappear constitute a *relapse* strain. Before the drug treatment one set of mice is subinoculated from the passage strain, and after treatment another series is subinoculated from the relapse strain. Now, if one of the mice be cured of its infection with the passage strain, it is immune to subsequent reinjections of the same strain, but it becomes infected and dies if inoculated with the relapse strain. Similar experiments can be carried out with the relapse strain. Immunity, therefore, toward the passage strain does not protect against the relapse strain, and *vice versa*, showing that the two are biologically different. The fact that the relapse strain is actually different from the original strain has been demonstrated in this manner by Ehrlich (1909), Ehrlich, Roehl and Gulbransen (1909), Rosenthal (1913) and Ritz (1914).

Of the papers mentioned, the one of Ritz (1914) is of particular interest. One of his mice was incompletely cured 20 times with the production of 17 immunologically different relapse strains. Some of these strains were identical with those of another mouse which had been incompletely cured 19 times with the production of 9 immunologically different strains. Thus, when the relapse strains in each mouse were numbered consecutively he found that No. 7 of the first mouse was the same as No. 3 of the second and Nos. 6, 9 and 8 of the first were the same as Nos. 4, 5 and 11 of the second, respectively. In over 600 mice he found 22 immunological variations.

Ehrlich, Roehl and Gulbransen (1909) and Ehrlich (1909) added another important contribution in that they found that trypanosomes could be made resistant *in vitro* to the trypanocidal antibodies which arise in mice after treatment. If mice were infected with the passage strain, cured, and then bled, their serum was found to be trypanocidal. If some of the original passage trypanosomes were now allowed to stand in contact with this serum for 15 minutes and then injected into normal mice, the trypanosomes from the resultant infection were found thereafter to be resistant to the trypanocidal serum. Furthermore, this resistance was retained for over a year, entailing over 200 passages through mice.

While these investigations were going on, other workers were studying the mechanism of relapse in uninfluenced infections where crises and relapses occurred naturally. The first systematic work on the lysins arising during the course of uninfluenced infections and their relation to crises and relapses was that of Rodet and Vallet (1906). Besides recognizing the lytic properties of the serum, these authors believe that certain organs, notably the spleen, have remarkable trypanolytic properties. Later work tends to show that this is not the case although Mutermilch (1911) has presented evidence that the trypanolysins are formed in the spleen and other hematopoietic organs. According to him, however, after these antibodies are thrown into the blood, the organs contain no more than can be accounted for by the blood in them. Similarly, certain authors have advanced evidence that phagocytosis

plays a significant part in the disappearance of the parasites, but from the literature, as well as from various unpublished experiments, the present author believes that such phagocytosis is a secondary phenomenon and that the trypanosomes which are phagocyted have already been injured, if not killed, by agencies present in the serum.

Massaglia (1907) showed that a definite correlation existed between the crisis and the lytic property of the serum. Thus, in a guinea pig before the crisis, the serum was only slightly lytic when tested on the same strain of trypanosomes, but the serum during and after the crisis was very strongly lytic to the original strain. Furthermore, he showed that although the serum taken after or during the crisis was strongly lytic to the original passage strain, it had no deleterious effect on the trypanosomes which reappeared in the guinea pig after the crisis to constitute the relapse. Here is clear experimental proof that the antibody which brought about the crisis remains in the blood (as shown by the activity against the original passage strain) and that the trypanosomes can accumulate again during the relapse due to a change in their biological properties which has made them no longer susceptible to the antibody. Massaglia then not only correlated the production of an antibody with the crisis but he explained the relapse in the uninfluenced course of the infection as being due to the acclimatization of the parasites to the antibody.

Levaditi and Mutermilch (1909), working with *T. brucei* and *T. evansi* in the guinea pig and using much more careful technique, confirmed Massaglia's general conclusions. They showed, furthermore, that when the trypanolysin acted on trypanosomes *in vitro* there was a coaction between a thermolabile nonspecific (alexin or complement) and a thermostable specific (sensitizer or amboceptor) property. They found, also, that between their two species the lysins were specific. They also state that the original passage strain can be made resistant to the lytic antibody by a few minutes contact with the immune serum *in vitro* (as Ehrlich, Roehl and Gulbransen, 1909, had previously done in their studies). This *in vitro* formation of resistant or relapse strains was very carefully studied by Levaditi and McIntosh (1910).

Leger and Ringenbach (1911*a* and *b*) studied the effects of various sera which were lytic to the homologous trypanosome upon heterologous trypanosome species. Although they found them to be in general specific they found the usual group relations manifested in such immunological phenomena.

Ritz (1916) has applied the method of Erhlich and his co-workers to the differentiation of relapse strains in the uninfluenced infection with *T. brucei* in the rabbit. He worked with a single-cell strain and obtained much the same results as he had previously obtained with mice in which the crises were artificially induced by partial cure with drugs.

Very little is known of the mode of formation of these antibody resistant races of the relapse. The explanation advanced by Ehrlich is an integral part of his general side-chain theory of immunity. He postulated that the protoplasm of the cell was composed stereochemically of a central molecular complex (Leitungskern) with which the basic activities of life were associated and a number of subsidiary molecular groups or side-chains (Seitenketten) with which the purely vegetative functions are associated. Of the side-chains those which could combine with chemical bodies were designated receptors or chemo-

receptors whereas those which combined more or less exclusively with food stuffs were differentiated as nutriceptors. His conception of the formation of a new race of trypanosomes resistant to antibodies is essentially that the nutriceptors of the original strain combine with the trypanocidal antibodies of the host and atrophy, whereupon new receptors are developed by the trypanosomes which will not combine with the antibodies in question, and hence, bring about a relapse. Ehrlich's explanation of the formation of *chemo-resistant* races of trypanosomes is different from this and depends, not on the atrophy of the nutriceptors, but on the modification of the corresponding receptors. In spite of the brilliancy of his experimental work, Ehrlich's hypothesis of "receptoric atrophy," though intriguingly simple, is nothing more than the re-statement of the experimental findings in figurative terms.

In the work of Levaditi and McIntosh (1910), when the immune serum from guinea pigs was added to a suspension of the passage trypanosomes, most of the parasites were killed and only a very few remained to be injected into mice to give rise to the resistant strain. This led Levaditi and McIntosh to postulate a process of true selection as the basis for the formation of antibody resistant strains. In the process the susceptible ones perished and the resistant ones repopulated the blood stream.

Rosenthal (1913) gives an hypothesis which really differs from either of the former in that he maintains that the trypanocidal substance in the serum is different from that which causes the trypanosomes to become resistant to the trypanocidal activity. The latter he terms the "relapse substances." This author tested the characteristics of his strains as follows: Mice were infected with *T. brucei*, cured with tartar emetic or arsacetin, and bled to give the immune serum possessing trypanocidal properties. To test the properties of the trypanosomes in a given mouse it was treated as above with tartar emetic or arsacetin and at the end of several days re-inoculated with the original strain. If it proved to be immune to the second injection, the trypanosomes of the original infection were said to have the properties of the original strain, if it proved not immune, the trypanosomes of its first infection were said to have the properties of the relapse strain. The author based his conclusions on three sets of experimental findings: (1) the trypanocidal property of mouse-immune serum does not vary proportionately to its power to produce relapse strains; (2) the property of producing relapse strains is thermolabile in that it is destroyed when the serum is heated at 60°C. for 15 minutes whereas the trypanocidal property is not altered by this treatment; and (3) the property of forming relapse strains is recovered with the albumen fraction of the serum whereas the trypanocidal property is recovered with both the albumen and the globulin fractions. If these findings are verified, particularly in the case of the trypanolysins arising in the uninfluenced infections in guinea pigs, etc., they will have a marked effect on our knowledge of the formation of these resistant strains.

Any acceptable explanation of the acquisition of a resistance to antibodies will have to take into consideration the fact that the phenomenon is very wide spread among both free-living and parasitic protozoa. The literature is too extensive to give more than a few of the more important developments. Among the trypanosomes, the same phenomenon occurs in regard to other immune properties developed in infected animals, such

as the "protective property" of immune sera. (See especially Mesnil and Brimont, 1909.) It occurs in treatment by drugs. Thus, if an infected animal is imperfectly treated with a trypanocidal drug and a relapse occurs, the trypanosomes are no longer susceptible to a dose of the same drug which would have cured the original infection. (See especially Erhlich, 1909. For a general review of these "induced variations" in the trypanosomes, see Dobell (1912).) Similar drug-resistant forms can be produced in the free-living species, *Paramecium*. (See Jollos, 1921.)

Certain facts are more or less common to all of these: (1) The acquisition of the resistance occurs within a "pure line" or single-cell strain. Consequently, if Levaditi and McIntosh mean to imply that a true selection of resistant genotypes from a "wild" population of mixed genotypes takes place, their explanation will not hold. (2) Although the resistance is inherited for many generations, it is lost in time. In the case of the parasitic forms, a change of vertebrate host in which it is grown or passage through the invertebrate host causes the strain to revert. In *Paramecium* it is generally quickly lost at conjugation (although it may survive one or two), but not at endomixis (Jollos, 1921). (3) Generally, even in Jollos' work on *Paramecium*, the acquisition of the resistance is associated with the killing off of a large part of the population and is acquired by the survivors very quickly. Thus, it seems to be something of a selection within the "pure line," but one selection is effective, a fact which is in marked contrast to the slow effects of selection of such characters as Jennings and others have studied in the free-living protozoa. (See Jennings, 1920.) The destruction, with its resulting selection, according to the work of Rosenthal, is not essential, but his results are difficult to apply to the acquisition of resistance to chemicals in the free-living forms. In addition to these general characteristics, it is interesting to note that in the case of the formation of chemical-resistant strains in single-cell strains of *Paramecium*, according to Neuschlosz (1919), the acquisition of a resistance to a chemical is associated with the acquisition of the power to destroy the specific chemical or to convert it into a less poisonous compound. Jollos has classified all of these cases of acquired resistance, together with certain other variations which are inherited for a greater or less time, as persistent variations or "Dauermodifikationen" and has thus differentiated them from true mutations.

V. INFECTIONS WITH THE NON-PATHOGENIC TRYPANOSOMES

Although by far the majority of trypanosome species exert no observable ill-effects on their hosts, the only one that has been carefully studied is *T. lewisi*, the non-pathogenic trypanosome of rats. The enumerative studies of Steffen (1921) showed that the number curve in this infection is generally as follows: After an incubation period, the parasites increase in the blood, sometimes attaining over several hundred thousand per cubic millimeter of blood, but if the rat does not die, there is a crisis in the early part of the infection when most of the parasites are destroyed; those that remain continue to live in the blood for some time (varying from several weeks to several months) until a second crisis occurs when all of them are destroyed. Rabinowitsch and Kempner (1899) showed that after the parasites disappear the rat is immune to a second infection. These results have

been fully confirmed by Taliaferro, W. H. and L. G. (1922), Taliaferro (1924) and Coventry (1925). (See fig. 5.)

Many years before exact enumerative studies were made on infections with *T. lewisi*, it was found from microscopical studies of slides made during the course of infections in the rat that during the first part of the infection, when the organisms are increasing in the blood, they are actively reproducing by fission but that during the latter part of the infection they simply exist in the blood as non-reproducing adults. This fact was clearly brought out by Rabinowitsch and Kempner (1899) and Wasielewski and Senn (1900). Laveran and Mesnil (1901) confirmed and greatly extended the observations of these earlier workers. Furthermore, the general cessation of reproduction was common knowledge to the protozoologists in succeeding years.

The retardation and final inhibition of reproduction was more accurately studied by the present author with the assistance of L. G. Taliaferro (1922). The progressive daily changes in the reproductive activity of the parasites throughout the entire infection with *T. lewisi* were clearly demonstrated by applying the coefficient of variation method, outlined previously. Thus, the daily rate of reproduction of the parasites was represented mathematically by drawing and measuring 100 parasites from each daily blood smear and calculating the coefficient of variation from these measurements. Coefficient of variation as used here means coefficient of variation for total length. Parenthetically, it may be recalled that the higher the rate of reproduction the higher the coefficient of variation will be. Thus, when the organisms first appear in the blood, microscopical examination reveals that they are reproducing at a very rapid rate and calculation for the coefficient of variation likewise gives the very high value of 25 to 30 per cent. The rate of reproduction on succeeding days, however, as expressed by the coefficient of variation, rapidly decreases (25.3, 18.8, 13.8, 3.9 per cent

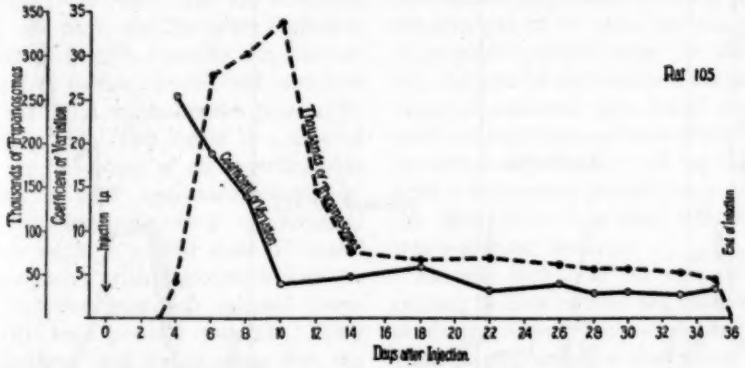
Rat 105
Thousands of Trypanosomes
Coefficient of Variation
Injection 1.0
Curve of Variation
Curve of Trypanosomes
End of Infection
Days after Injection
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36
50 100 150 200 250 300 350
5 10 15 20 25 30 35

FIG. 5. GRAPH SHOWING THE COEFFICIENT OF VARIATION FOR TOTAL LENGTH (COMPARATIVE MEASURE OF THE RATE OF REPRODUCTION) AND THE NUMBER OF TRYPANOSOMES PER CUBIC MILLIMETER OF BLOOD, THROUGHOUT THE COURSE OF AN INFECTION WITH T. LEWISI IN A RAT

This infection illustrates the condition in which there are both an inhibition of reproduction of the parasites, as shown by the drop in the coefficient of variation to about 3 per cent by the tenth day, and a marked parasiticidal action, as shown by the number crisis about the twelfth day and at the end of the infection. (After W. H. Taliaferro.)

the fourth, sixth, eighth and tenth days of the blood infection, respectively) until about the tenth day of the infection when no reproduction is found to be taking place at all, at which time the coefficient of variation is around 3 per cent. Reproduction is never resumed thereafter; that (1) the retardation and final inhibition of reproduction by about the tenth day, (2) the sudden destruction of the majority of the parasites between the eighth and twelfth days, and (3) the eventual total destruction of the parasites which terminates the infection and may take place

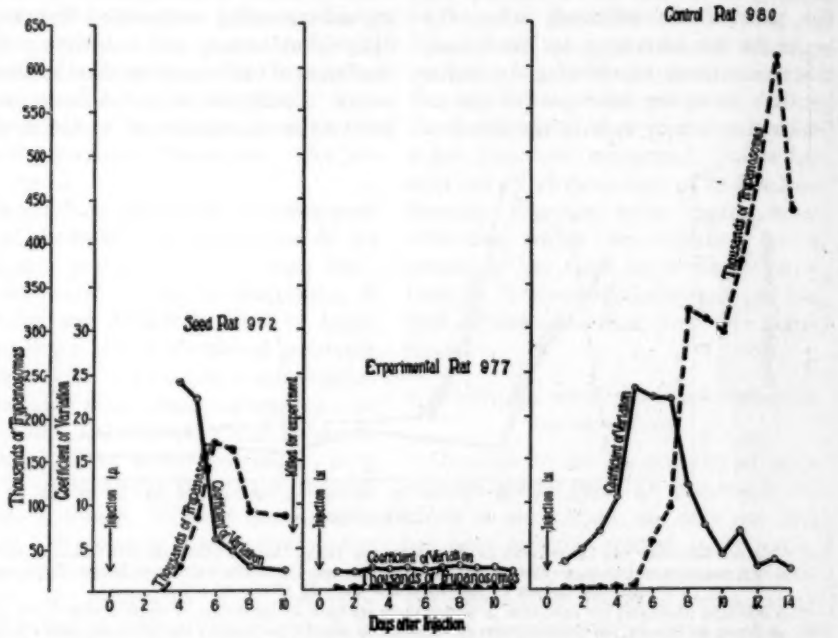

FIG. 6. GRAPHS DEMONSTRATING THE PASSIVE IMMUNIZATION OF AN UNINFECTED RAT WITH THE REPRODUCTION-INHIBITING REACTION PRODUCT WHICH HAS BEEN FORMED IN AN INFECTED RAT

Note that after reproduction had been inhibited in Seed Rat 972, one half of its adult trypanosomes, plus a suitable amount of its serum, was injected into Experimental Rat 977, while the other half of its trypanosomes, plus an equal amount of serum from a *normal* rat, was injected into Control Rat 980. Subsequently, in Experimental Rat 977 the normal cycle of reproduction was altered—there was a complete inhibition of reproduction as evidenced by the coefficient of variation; whereas in Control Rat 980, the normal cycle of reproduction took place. (The peak in the number curve of Control Rat 980 is so much higher than that of Seed Rat 972 because it received an enormously large number of parasites initially.) (After W. H. Taliaferro.)

is to say, the coefficient of variation remains in the vicinity of 3 per cent throughout the remainder of the infection, which may, in some cases, as previously stated, extend over a period of several months.

From this work it may be said that there are three manifestations of resistance: from a few days to several months after the first crisis.

The immunological basis of the first effect of resistance has been studied by the present author (1924). His work indicates that the inhibition of reproduction is due to the acquisition of a property of

the serum in the infected rat which has the peculiar property of inhibiting reproduction but which does not kill the trypanosomes. The method of demonstrating the presence of this property or reaction product is shown in figure 6 which is an example from numerous experiments carried out by the author (1924) and Coventry (1925). First, an infection in a rat (seed rat 972) was allowed to progress until the tenth day when the parasites were no longer reproducing and the coefficient of variation was in consequence 3 per cent. The rat was then killed and bled, and its serum collected. The serum (which contains the reaction product or immune body) was separated from the adult trypanosomes present by centrifugation. This serum in a dose of 2 cc. per 100 grams of rat together with half of the adult trypanosomes was injected intravenously into experimental rat 977 while a similar dose of *normal* serum together with the other half of the adult trypanosomes was injected intravenously into control rat 980. Daily examinations and calculations for the coefficient of variation for total length for these two rats showed that the trypanosomes in experimental rat 977 lived in the blood for eleven days (infection died out at this time) without showing any reproduction (the coefficient of variation never exceeded 3 per cent, and furthermore, the organisms never increased in the blood and no dividing parasites could be found); whereas in control rat 980 reproduction began on the second day and followed the course of a normal infection (the coefficient reached the high peak of 25 per cent between the fourth and sixth days, and as was to be expected, the organisms showed a marked increase in numbers in the blood and many dividing parasites were found). In these experiments it is to be noted that not only did the immune serum, viz., the serum taken from the seed rat on the tenth day, prevent "adult" trypanosomes from reproducing in a new rat, but that normal rat serum did not prevent similar adult parasites from reproducing in a similar new rat. This is a clear-cut case of the passive transfer of the immunity from an infected to an uninfected rat.

The changes in titer of this reaction product through the course of an ordinary infection has been studied in detail by Coventry (1925). She was unable to demonstrate its presence in serum prior to the fifth day of the infection although it is probably present since by the fifth day the rate of reproduction has already begun to decrease. She found a sudden and very great increase in its titer between the fifth and sixth days of the infection with a subsequent gradual increase until the thirty-fifth day after which there was a gradual decrease.

As the formation of this reaction product, which inhibits the reproduction of the parasites without affecting their vitality, emphasizes a new effect of resistance, the present author has attempted to compare it with other known immune bodies (unpublished work and Taliaferro, 1925). Like most reaction products or antibodies, this one is nonether soluble and is precipitated with the globulin fraction of the immune serum. Strange to say, it comes down equally with the eu- and pseudoglobulin. It differs from others, however, in its lack of *in vitro* affinity for its supposed antigen. Thus, when serum containing it is left in contact for 12 hours with large numbers of dividing *T. lewisi* and the parasites subsequently removed, the serum does not lose any of its titer.

As far as the author is aware there has been neither any experimental work nor any explanation advanced to account for

the second manifestation of resistance, i.e., the first number crisis which occurs between the eighth and twelfth day of the infection.

Some work, however, on the immunological basis for the immunity of recovered rats to a second infection with *T. lewisi*, has been done and probably explains the third manifestation of resistance, i.e., the crisis which terminates the infection. Laveran and Mesnil (1901) came to the conclusion that this immunity as well as the final disappearance of the parasites is due to the phagocytosis of the living trypanosomes. MacNeal (1904), on the other hand, has obtained experimental evidence that the final disappearance of the trypanosomes is due to a trypanolytic process, just as has already been described for the crises in the pathogenic forms. Manteufel (1909) also holds that phagocytosis is only a secondary function and that the immunity rests upon the trypanocidal or trypanolytic property of the serum. The present author (1924) has confirmed MacNeal's work that a lysin is formed at the termination of the infection. His work indicates, however, that this lysin which terminates the infection disappears from the blood and is not the basis of future immunity, but that this is bound up with the reproduction-inhibiting reaction product described above. Let us consider how this might be. A rat recovered from an infection of *T. lewisi* possesses, let us say, in its blood-stream the reproduction-inhibiting reaction product but no trypanolysin. Under ordinary conditions it receives comparatively few forms from either injection or from infected fleas. These find their way, eventually, into the blood and exist there, at least for a time, but being unable to reproduce, can not set up infection. During this time even though examinations of the blood are made no trypanosomes are found because they have been dispersed throughout the rat. The reproduction-inhibiting reaction product, therefore, prevents the occurrence of a normal infection although it allows a few stray forms to live on in the blood.

VI. COMPARISON OF THE LETHAL AND NON-LETHAL TRYPANOSOMES

A consideration of all of the known trypanosome species brings out the fact that most of them are, as far as can be seen, non-pathogenic parasites (commensals) just as *T. lewisi* is in rats. There is a growing mass of evidence that even many of the well-known pathogenic forms, which produce such fatal diseases in man and domesticated animals, live as non-pathogenic forms in their natural vertebrate hosts. Thus, *T. gambiense* may be a harmless commensal of the antelope and other wild game of Africa. This at once leads to the suggestion that whether or not a given species is pathogenic depends upon the reactions of the host. A comparison of the resistance which a host acquires against the pathogenic forms and the resistance of the rat against the non-pathogenic *T. lewisi* is very interesting in this connection. It has been seen that in the pathogenic trypanosomiases, the host either acquires no resistance (mouse) or periodically forms a trypanolysin which produces a number crisis (guinea pig, dog, etc.). In the second case, the resistance is never permanently effective because the parasites are never all killed and those which remain, after becoming resistant to the antibody, can continue to reproduce at an uniform rate. In the non-pathogenic *T. lewisi*, however, the host first produces an antibody which completely inhibits reproduction (cell-division) in the parasites. Thereafter, each number crisis is so much gained by the host be-

cause the parasites cannot re-populate the blood stream even if they should become resistant to the trypanocidal mechanism. It is possible then that the formation of a reproduction-inhibiting reaction product, in conjunction with trypanocidal antibodies, would convert an otherwise lethal parasite into a non-lethal one. Van Saceghem (1923) suggests that the presence of such a reproduction-inhibiting property causes the pathogenic trypanosomes to become harmless commensals in wild animals. Brown (1914*a* and *b*) has studied a strain of *T. lewisi*, which was pathogenic to rats. In considering his second paper, the chief anomalies of his pathogenic strain can be explained on the assumption that it continued to reproduce much longer than normal strains. This indicates that in a rat no longer capable of forming the reproduction-inhibiting antibody, the parasite becomes pathogenic. Similarly, the author has observed apparent lethal infections with *T. lewisi* in which the reproduction of the parasites was never completely inhibited.

Another example of the so-called pathogenic trypanosomes becoming non-lethal to their hosts is seen in the Bovidae. Most of our knowledge of this type of infection, which has been fully described by Laveran (1911) and Mesnil and Leger (1912), has been derived from work on goats and sheep where the infection is generally of such a low grade that the parasites can not be found by microscopical examination but their presence can be demonstrated by subinoculations into mice. Such an infection persists for from one to several months whereupon the host recovers and is more or less refractory to a second infection with the same species of trypanosome. It is, of course, impossible to analyse the effects of resistance in this type of infection as we have done in the preceding infections because the trypanosomes can not be found microscopically in the blood. Similarly, there is little indication of what the immunological basis for this type of infection may be.

One outstanding feature of the serum of animals that show a chronic (viz., sheep) or even sub-acute (viz., the rabbit) infection is that it is *protective*. If serum from such an infected animal be injected simultaneously with trypanosomes from the passage strain, it will either delay or completely inhibit the infection. Such serum is not curative, i.e., it does not prolong the life of mice if injected after the infection has progressed for even a day or so.

This immune property will only be mentioned since, so far, there is no direct evidence that it is connected with, or is the basis for, the chronic or low grade type of infection. The protective property of immune serum was probably first observed by Rouget (1896) who found that the serum of rabbits and dogs which were infected with *T. equiperdum* and had become cachetic exerted a protective action on mice infected with the same trypanosome, as measured by their survival time. By far the most careful work on it was done by Mesnil and Brimont (1909) who worked with *T. evansi*, *T. brucei* and *T. togolense* (= nagana of Togoland).

In the consideration of the pathogenic trypanosomes in various laboratory animals, it has been stated repeatedly that reproduction occurs uniformly throughout the infection. Some of the work of Robertson (1912) on *T. gambiense* in the monkey indicates that an endogenous cycle of reproduction occurs in which phases of active reproduction alternate with phases of lessened reproduction. She measured the rate of reproduction by ascertaining the percentage of dividing

forms on successive days—a method which is undoubtedly valid but which possesses a drawback in that the comparative scarcity of dividing forms makes it difficult to obtain statistically valid samples. With her data, however, which contains the length of trypanosomes from day to day, the present author has applied his coefficient of variation method and has found that Robertson's conclusions are sound, but that even at the periods of least reproduction, reproduction is nevertheless occurring at a comparatively high rate.

VII. MALARIAL INFECTIONS

Among the malarial parasites, the most complete knowledge of the course of the infection has been obtained from a study of *Plasmodium relictum*, the parasite of sparrows and probably of other birds. This is due to the fact that this organism is well-adapted to laboratory work not only because it is easily grown in the domestic canary but can be transmitted from one bird to another by injections of infected blood. Our knowledge of the

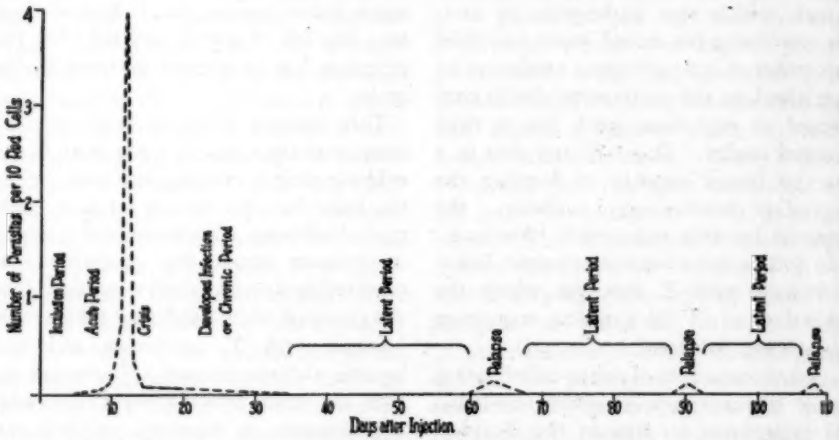

FIG. 7. GRAPH ILLUSTRATING THE COURSE OF AN INFECTION OF PLASMODIUM RELICTUM IN THE CANARY

Furthermore, there is some evidence that the original strains of parasites in Africa show these alternate phases of reproductive activity, but that by continuous subinoculation in the laboratory, the rate becomes constant. Consequently, although Robertson's results are of a great theoretical interest, they do not invalidate the general deductions made in this and other sections on the pathogenic trypanosomes, since reproduction was never completely and permanently inhibited, as in the case with *T. lewisi* in the rat.

progressive changes in the number of parasites in the blood has accumulated from the work of many investigators. Exact enumerative studies have been made by the Sergents (see especially 1918), Ben Harel (1923), Taliaferro, L. G. (1925) and Boyd (1925).

In general the course of the infection may be divided into the following periods, as is shown in figure 7: (1) After the introduction of the parasites (whether by the bite of a mosquito or injection) there is an incubation period during which no

parasites can be found in the blood and the length of which is, according to Boyd, largely correlated with the number of parasites received. (2) The acute stage is initiated when they appear in the blood and extends over a period of 3 or 4 days (sometimes more) during which the parasites are rapidly increasing in number. According to L. G. Taliaferro (1925), the rate of this increase is uniform and follows the formula for a geometrical progression series. Even during this acute period when the number of parasites are increasing most of the young merozoites produced at each sporulation die (L. G. Taliaferro, 1925). Hartman (1926) has made a very careful study of the mortality at this time. (3) If the bird does not die, the acute period is terminated by a crisis which sweeps the majority of the parasites from the blood. Sometimes there may be several acute rises in the number of parasites, each followed by a crisis. (4) Following the crisis, a low grade infection ensues which is variously termed the chronic stage or the developed infection. During this period, comparatively few parasites are found in the blood although they may fluctuate in numbers to a certain extent. (5) In time all of the parasites apparently disappear from the blood and give rise to what is termed the latent period. Although they cannot be found, a few parasites must be present since Whitmore (1918) has shown that blood taken at this time is infective to other birds, and Mazza (1924) has found a bird infective 4 years and 2 months after infection. (6) At any time during the latent period the injection of adrenalin or any condition which lowers the bodily resistance of the host, such as exposure, etc., may cause the parasites to reappear in the blood. Such a reappearance is called a relapse.

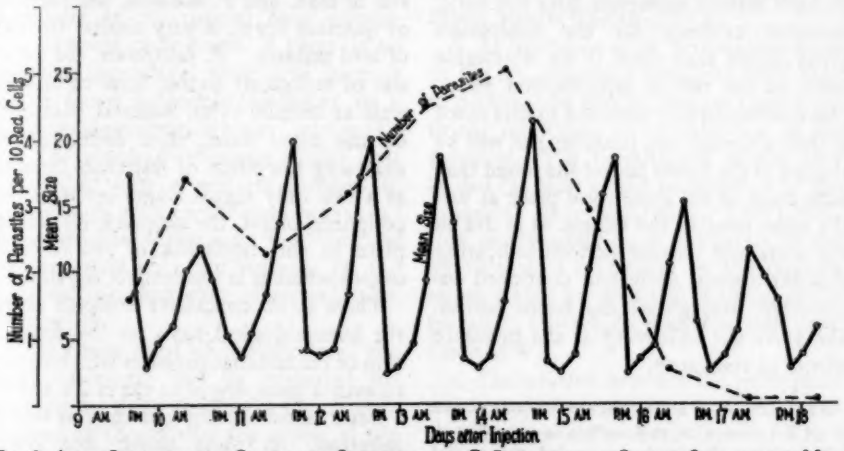

FIG. 8. ACUTE INFECTION AND CRISIS IN AN INFECTION WITH P. RELICTUM IN A CANARY SHOWING THE MEAN SIZE OF THE ASEXUAL FORMS AT 4-HOUR INTERVALS AND THE NUMBER OF PARASITES PER 10 RED BLOOD CELLS

The distance between peaks of the mean is a measure of the rate of reproduction which is independent of the number of parasites destroyed. (From data by L. G. Taliaferro.)

The number crises which terminate the acute, chronic and relapse periods leave little doubt that some type of resistance is acquired which destroys large numbers of the parasites after they are formed. Unlike *T. lewisi*, however, this is not associated with any retardation of the

rate of reproduction of the parasites according to an extensive study made by L. G. Taliaferro (1925). By using, as a measurement of the rate of reproduction, the length of time necessary for each asexual generation, which has already been explained, she found that no matter when the organisms are studied, whether in the acute, chronic or relapse periods, the length of the asexual cycle is the same (24 hours in one strain). This fact, in conjunction with the fact that the average number of merozoites produced by each mature segmenter does not vary, furnishes evidence for the conclusion given above that there is no noticeable effect on the rate of reproduction *per se*. One interesting fact disclosed in this work is that although the parasites can not be studied in the latent period she found that each stage in the cycle took place at just the same time in the relapse as it did in the acute and chronic periods indicating that the asexual cycle had continued undisturbed throughout the latent period. She gives the following as the probable effects of resistance.

> In conclusion, it seems that the probable picture of an infection with bird malaria is somewhat as follows: After the incubation period the asexual stages of the parasites are to be found in the peripheral blood in varying numbers during the entire course of the infection and undergo their cycle of development and reproduction at the same rate throughout. From the very beginning, only a number of the merozoites are viable; this probably represents a natural resistance of the host. During the first part of the infection relatively few parasites are killed, so that they accumulate in the blood and give rise to the acute stage of the infection. Sooner or later, however, as the acquired resistance is built up, a large proportion of the parasites are killed. There may then be a temporary relapse, but eventually the destruction of the parasites equalizes or exceeds the number produced by reproduction, and the chronic period or low grade of blood infection ensues. In time, the destruction becomes so great that no parasites can be found in the blood (latent period), but their presence can be demonstrated by Whitmore's technique. This continues until some condition, such as the injection of adrenalin, temporarily stops the destruction and the parasites accumulate again, causing a relapse.

It is difficult to study uninfluenced infections of malaria in man because most of them are treated with quinine. Ross and Thomson (1910*b*) have, however, made a very precise enumerative study of the human infection. From the general experience of most workers it seems probable that the course of the infection of both *P. vivax*, the benign tertian parasite of man, and *P. malariae*, the parasite of quartian fever, is very similar to that of bird malaria. *P. falciparum*, the parasite of malignant tertian fever of man as well as certain avian malarial parasites, on the other hand, offer difficulties in analysing the effect of resistance because as a rule only sexual stages occur in the peripheral blood, the asexual cycle taking place in the capillaries of the internal organs where it is inaccessible for study.

There is no conclusive evidence as to the immunological basis for the destruction of the malarial parasites which occurs to such a great degree at the crises and to a lesser extent throughout the rest of the infection. At these times, Ben Harel (1923) has noted a marked increase in the number of large mononuclear phagocytes in which, furthermore, she has observed some evidences of parasitic phagocytosis. Consequently, she believes that the increase in mononuclears is associated with the decrease of the parasites. It is also a well-known fact that after the crisis, a marked splenomegaly occurs, and that large numbers of parasites in various stages of disintegration can be found in the spleen during this time. No evidence is at present available, however, to show whether these wandering mononuclears and fixed-tissue phagocytes of the spleen and other organs are the pri-

mary cause of the destruction or are simply clearing up debris in the form of parasites already killed by some other agency.

VIII. CONCLUSIONS

As this review is itself essentially a summary, the author will list here only a few of the more salient facts which have been brought out by the present discussion. The authorities for these statements may be found under the sections listed at the end of each statement.

1. After blood parasites, such as are considered in this paper, have successfully invaded their hosts, if there is no resistance operative, they will increase in the blood uniformly according to a geometrical progression series (Section II).

2. The acquired resistance of the host can modify such a uniform increase in one or both of two different ways: (1) by parasiticidal effects, i.e., by killing the parasites after they are formed; or (2) by inhibiting their rate of reproduction (Section II).

3. The sum total of the effects of the host's resistance can be evaluated by studying the daily changes in the number of parasites throughout the course of the infection. By using indirect measures of the rate of reproduction of the parasites (coefficient of variation for total length in the trypanosomes or changes in mean size in the malarial organisms), in conjunction with the number curve, the two effects of the host's resistance can be differentiated (Section II).

4. In the pathogenic trypanosomes in the mouse, the host acquires no appreciable resistance, either affecting the rate of reproduction or exerting parasiticidal effects on the trypanosomes (Section III).

5. If the same pathogenic trypanosomes are grown in such hosts as the guinea pig, there is no effect on the rate of reproduction, but there are parasiticidal effects causing periodic number crises. These crises result from the production of trypanolysins. These lysins remain in the blood, and, if the host does not die, the parasites become changed biologically so that they are resistant to the antibody, and hence, are able to re-populate the blood stream (Section IV).

6. In infections with *Trypanosoma lewisi* in the rat, resistance manifests itself both in parasiticidal effects (number crises) and in the inhibition of reproduction of the parasites. The parasiticidal effects may be due (at least at the termination of the infection) to trypanolysins. The inhibition of reproduction is the result of the acquisition of a property by the immune serum which prevents cell division of the parasites, but which does not kill them (Section V).

7. The relation between the pathogenic and non-pathogenic trypanosome infections is discussed in detail (Section VI).

8. In the malaria parasite of birds (*Plasmodium relictum*), a marked parasiticidal effect of resistance is manifested both at definite number crises and throughout the latter part of the infection. This is, however, not associated with any inhibition of the reproduction of the parasites. The immunological basis for the parasiticidal effects are not definitely known (Section VII)

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FREEZING AND SURVIVAL OF INSECTS AT LOW TEMPERATURES

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EXTREMES of temperature are important factors in the ecology of all animals. Low temperatures affect the geographical distribution of insects, their cold resistance, rate of metabolism, behavior, and in some cases even their color and structure. This paper is the result of studies of the effect of low temperatures on cold resistance in insects with especial reference to temperatures below the freezing point of water.

Three ecological groups of insects were chosen for study: (1) the oak borers living close to the outer surface of the bark, normally exposed to extremes of low temperature; (2) aquatic insects living in lakes, never exposed to temperatures lower than 0°C.; (3) insects infesting stored products.

The necessity for the endurance of low temperature is a fundamental one which must be met by all organisms living in Northern climates. The literature on the biological effects of low temperatures is enormous. Literature relating to both plants and animals is cited in this paper for the reason that plant physiology has been advanced to a farther stage than insect physiology and offers many suggestions to workers in the animal field.

I. LITERATURE ON THE EFFECTS OF LOW TEMPERATURE ON PLANTS

There is an extensive and scattered literature on the freezing and hardening in plants and on allied physiological effects of cold. It is interesting to discover that very early in the history of plant physiology, observations took on a quantitative aspect. Workers in this field of plant physiology include some of the foremost plant physiologists, as for example, Sachs and Pfeffer.

In plants, death from freezing has been considered to be due to the following causes: (1) mechanical injury from ice crystal formation, (2) water loss either direct or indirect through permeability changes in the cell membrane, (3) precipitation of proteins or other irreversible chemical effects. The order given in general follows the historic development of the study of cold effects on plants.

Duhamel and Buffon (1732) held that death from freezing was due to the rupture of tissue from ice crystals formed in freezing. Morren (1852) found no histological evidence in favor of this theory. Göppert (1829) found that ice formation took place in both cells and cellular spaces. Sachs (1860) discovered that in the process of freezing water was withdrawn from the cells to freeze for the most part in the intercellular spaces. From another source evidence was obtained against the cell-rupture theory when Nägeli (1860) calculated the expansion of all the water in a cell at freezing and found that the total expansion was insufficient to cause rupture. However, disproving that cell rupture is the cause

of death from low temperatures is not the equivalent of finding the cause of death from low temperatures, nor does the negative result obtained throw much light on the subject of death from this cause.

Water loss both direct and indirect was the next explanation for injury and death at low temperatures. Water loss from frozen tissue on thawing was observed by Göppert (1829). Prilleux (1869) discovered that water was exuded from the cells in the freezing process. Sachs (1860) noted that water exuded from the cells was "reabsorbed" or was lost by evaporation. Injury from freezing was thought to be due essentially to a dehydration. Another effect of low temperature analogous to the effect from freezing was dehydration at low temperatures above the freezing point. Water intake and water transportation at low temperatures is not rapid enough to balance transpiration. The plant exposed to such temperatures may wilt and finally die from the effects of low temperature without ever being frozen. Sachs (1860) points out these two dehydration effects of low temperature.

As an outgrowth of the more simple theory of direct water loss comes the theory of injury from water loss due to alteration of the permeability of the cell membrane at the time of freezing. Loss of water according to this view is not the primary cause of death from freezing, but permeability changes are. Maximow (1912) worked on sections of red cabbage and *Tradescantia*. He came to the conclusion that the part of the plant that was injured by low temperature was the plasma membrane. The immersion of sections of plant tissue in various solutions influenced the freezing point. Substances that enabled the cells to withstand a lower temperature than normally were called "Schützmittell" or protective substances. The degree of protection afforded by different substances was proportional to the eutectic point when the molecular concentrations were the same. Chandler (1913) came to the conclusion that the cause of death from freezing was due to mechanical injury of the plasma membrane. Death from freezing was limited to one condition, namely, the condition of brown wilted tissue resulting from exposure to freezing temperatures and subsequent thawing. Poor metabolism due to low temperature was not studied in Chandler's paper.

The third theory considers protein precipitation in the frozen cells accountable for death from freezing. The first man to elaborate this theory was Gorke (1906). His evidence was derived from plant cells and from solutions of proteins. The degree of hardiness in plants was correlated with the ease or difficulty with which their proteins were precipitated. In non-hardy begonia leaves protein precipitation took place at −3°C., in rye at −15°C., and in pine needles at −40°C. Schaffnit (1910) found that rye protein from plants grown under greenhouse conditions was more easily precipitated than rye protein from plants grown under outdoor conditions. Schaffnit's work will be taken up again when hardiness is discussed. Harvey (1918) found that a correlation existed between protein precipitation and hardiness. The influence of increased sugar content noted by Lidforss (1907), by Schaffnit (1910), and by later workers may be primarily as a protection to the proteins against precipitation, although such solutes would also lower the freezing point. Harvey (1919) laid emphasis on the relation of epidermal coverings to undercooling. He considered that concentration of cell solutes played a minor rôle in the determination of cold resistance in plants, the

principal effect coming from the precipitation of protein under the changed conditions produced by ice formation.

The development of hardiness in plants and the correlation of physical condition of cell colloids and of osmotic concentration of solutes with hardiness, is at present one of the extensively cultivated fields of plant physiology. By hardiness is meant the resistance of plants to low temperatures. Harvey has defined this term as the ability of a plant to survive ice formation within the tissues. The present writer uses the more general definition given first on account of the fact that the term hardiness has been used in the broader sense in much plant literature, and also for the reason that cold resistance in animals has not been studied sufficiently for us to know definitely the underlying cell changes that are responsible for increased resistance to cold.

Plant hardiness has long been of interest in horticulture and agriculture. Efforts to produce frost hardy plants are some of the new developments arising from the application of plant physiology and genetics. Factors that make for plant hardiness were studied in detail by Gorke (1906). Schaffnit (1910) found that cold hardiness in rye was increased by exposure of rye to low temperatures during growth. Lidforss (1907) noted that the sugar content of pine needles increased with the oncoming of winter. Maximow (1912) found that he could induce hardiness in plant tissues by soaking them in solutions of non-toxic substances. Among the substances used were glycerine, sucrose, mannite, and various nitrate salts. Rosa (1921) comes to the conclusion that any process which will bring about a material decrease in the rate of growth will result in an increase in hardiness. Decreasing the water content, increasing the amount of hydrophylic colloids present or increasing the water holding capacity of these colloids will result in an increase of hardiness, according to this investigator. Harvey (1918) studied the development of hardiness in plants and comes to the following conclusion.

> The principal effect of the hardening process for cabbages is a change in the constituents of the protoplasm which prevents their precipitation as a result of the physical changes incident upon freezing. The proteins are changed to forms which are less easily precipitated. This is indicated by an increase in the amino-acid content of the cabbage plants on hardening.
>
> . . . . The effects of desiccation, freezing, and plasmolysis are considered to be similar in that all these processes cause changes in the hydrogen-ion and salt concentration.

Studies on the concentration of the sap and its relation to hardiness have been made by Gortner and Harris (1914). Tropical plants have a lower osmotic concentration and a lower pressure than do plants of temperate zones. Newton (1924) worked on the relation of the concentration of cell sap to the winter killing of different varieties of wheat. The ability of the cell colloids to adsorb water was taken as a measure of the cold resistance of winter wheat. The process of hardening in this case is thought to be the process of water adsorption and water retention by the hydrophilic colloids.

The relation of water content to winter hardiness was stressed by Johnson (1919, 1921, and 1923). He used water content as an index to the hardiness of peach buds. Newton (1924) found that water content of winter wheat was a partial index to hardiness.

There is another aspect to the subject of freezing that was brought out by Müller-Thurgau (1880). He distinguished between freezing and death from freezing. He also contributed to the theory of

freezing and made valuable observations on low temperatures of trees in winter.

Göppert (1839) held that rapid thawing would cause death after freezing but slow thawing would enable plants to survive. He cited examples of saving plants by thawing them in cold water. Müller-Thurgau (1880) compared the rate of thawing in air and in water of the same temperature and found that the rate of thawing in water was greater than the rate in air. A wide series of plants were tested for injury after slow thawing and after rapid thawing. Some plants showed typical spots of frost injury but were not killed, others showed no injury, and still others were killed outright. Müller-Thurgau (1880) concluded that rate of thawing was not closely correlated to survival after freezing, and that plants that would be killed by rapid thawing could not be saved by slow thawing.

Müller-Thurgau (1880) figures ice crystals in his first paper and also "Eisdrüsen" or ice glands—centers of crystallization. He also gives a method for determining the amount of water formed into ice. He concludes that there can be no freezing to death without first ice formation. Death does not precede freezing but follows it. He also gives extended figures on the winter temperatures of the north and south sides of trees, and shows the alternate freezing and thawing to which trees are subjected. This last phase of his work is important in the present considerations for the oak borers are exposed to the same conditions as the trees which they inhabit.

Müller-Thurgau (1880, 1886) found that plant sap froze at higher temperatures than the whole plant. He explains this higher freezing point on the basis of capillarity and structure of protoplasm. The intact plant is able to hold its water and prevent part of it from freezing. Altogether these papers of Müller-Thurgau form one of the most important contributions to plant freezing and hardening. He also made some general observations on freezing in animals. On account of the importance of the study of tree temperatures in the study of the oak borer group, the following work is quoted. Emerson (1889) studied the temperatures of tree trunks in Nebraska. Squires (1894) and later Harvey (1923) studied the temperatures of trees in Minnesota. Graham (1920, 1922), made a study of tree temperatures with special reference to the maximum temperature endured by insects living under the bark. The influence of the color of the bark on the temperature of the cambial layer was stressed by both Graham and Harvey. Black bark has a higher temperature at a given air temperature than white bark. In winter, according to Harvey, there may be as much as 25°C. difference between the temperature of the north and of the south sides of trees. Alternate freezing and thawing of a living cambial layer is produced by alternation of sunlight and shadow when a cloud passes.

II. LITERATURE ON THE EFFECTS OF LOW TEMPERATURE ON ANIMALS WITH SPECIAL REFERENCE TO INSECTS

The progress of low temperature studies on insects has not been as rapid, nor has the quantitative aspect been emphasized as much as has been the case in plant physiology. The large economic losses from tender plants and the consequent desire to develop hardy varieties have had no counterpart in applied entomology, with the exception of some work concerning the insecticidal effects of low temperature over given periods of time.

The problem of hardiness in insects is essentially a part of the problem of hibernation. Animals that live in cold cli-

mates must adapt themselves to the conditions as they are, or avoid these conditions by migration to warmer or better protected places. This paper deals with animals that are so situated that they cannot avoid the low temperatures of winter but must take the temperature just as it is.

Allied to the problem of hibernation is the question of heat regulation which plays an important part especially in the hibernation of mammals. Rasmussen (1916) gives a summary of the different theories of hibernation. During hibernation homoiothermal animals become poikilothermic. In this latter state they are able to endure cold and starvation which under other conditions would be fatal. The hibernation of mammals may throw some light on the allied problem, the hibernation of insects. Low temperature, high concentration of carbon dioxide, and periodicity, were the chief factors proposed as causes of hibernation. An incompletely homoiothermic mechanism was associated with hibernation. The influence of low temperature on the production of a state of lethargy holds for insects as well as other animals. Periodicity has been emphasized by many workers. The question of a heat regulating mechanism is not fully settled, but there is some evidence from the work of Newport (1837), Bachmetjew (1901), and Pirsch (1923) that insects do have a slight control of their bodily temperatures under different environmental conditions.

The earliest literature on insect hibernation is gleaned from collectors' notes and simple observation that insects are found at low temperatures or do pass the winter out-of-doors. These notes will be passed over, as they do not contribute vitally to the subject in hand.

Aristotle knew that insects hibernated, but did not seek an explanation for this phenomenon.

One of the most striking characteristics about the state of hibernation is its periodicity. Even the name suggests this characteristic. Kirby and Spence (1818) view the phenomenon of hibernation as periodic, although this is not explicitly stated. The action of cold it is pointed out is not sufficient to account for the state of hibernation. Insects in hibernation, it is noted, are able to withstand extremes of low temperature, fatal to them in the active state. The statement is also made that insects frozen as solid as a block of ice can live after being thawed out, but that some insects die from the effect of cold before the freezing point is reached. Hibernation is looked upon as a provision against starvation at a time when the food of insects, whether herbivorous or carnivorous is no longer obtainable.

Baumberger (1917) makes much of the factor of periodicity. Hibernation, according to this author, is essentially a rhythmic phenomenon. It does not occur in tropical insects and is not well fixed in animals more or less protected from winter temperatures. The most fixed and the most periodic hibernation periods occur in animals exposed to winter temperatures habitually.

The meaning of the state of hibernation especially in regard to change or lack of feeding in this state was observed experimentally by Réaumur (1740) and by Huber (1792) in bees. Bees were observed to be active inside their cluster throughout the winter. Réaumur observed that less food was eaten by a hive kept in the cold than one kept in a warm place. Clustering, according to this author, was a manifestation of torpidity. Huber considered that the winter cluster was not the result of torpidity but rather a means of avoiding torpidity by keeping the temperature high.

The state of lethargy in caterpillars was observed by Vaudoner (1817). He noted especially its essential periodicity and observed that this state was not due entirely to lack of food or to low temperatures. Vaudoner's work has been largely overlooked by later biologists. Scudder (1889) found that some caterpillars went into a state of lethargy or premature hibernation at midsummer. Others continued feeding till the onset of severe weather. Between the state of hibernation and activity were shorter and less completely passive periods in the life of some caterpillars. The idea of hibernation as a comparative state rather than an absolute state is here expressed though not explicitly. This idea will reappear again when the subject of cold resistance is taken up. Hibernation of partial broods is considered by Scudder as a means for preserving the species. Thus if part of a group of feeding caterpillars go into a state of lethargy at one time and part at another, the chances for the survival of the species is better.

Associated with hibernation are other low temperature effects such as the freezing point of insects under different contions, undercooling, hardiness, and lowered rate of metabolism. The rate of metabolism will not be discussed in this paper except in so far as it bears directly on the general problem of hardiness.

The observations of cold resistance in insects are scattering and often indefinite. A certain insect seen on a cold day, or revived after being exposed to winter temperatures, is a common type of observation. However, not all the observations are of this indefinite kind, for Réaumur, who was interested in temperature, was making measurements of the temperatures borne by some little larvae found in wood. Réaumur (1736) placed small larvae in a freezing mixture of marine salt and water. The larvae were placed in a glass tube and the temperature of the freezing mixture taken. Larvae were able to withstand −8° or −9° Réaumur without perishing. These experiments were performed in the years 1708 and 1709 but were published in his monumental work *Mémoires pour servir à l'Histoire des Insectes*. In this work he also quotes an experiment of Lister who found that insects frozen so hard that they sounded like stones when dropped into a glass survived. This experiment has been requoted many times and has entered into current thought regarding the subject of survival from freezing. The fact of becoming stiff, even hard, may not be a proof that the insect is actually frozen, although workers today as well as in the 18th century, assume the two states to be identical.

The taking of individual temperatures of insects was first accomplished by means of small mercury thermometers. Davy (1816), Rengger (1817), Regnault (1819), and Hausmann (1803) were pioneers in this work. Newport (1837) conducted extensive studies on temperatures of insects of several species and representing four orders. These workers laid the foundation for later work on insect temperature and cold resistance.

By far the most comprehensive work dealing with the subject of insect temperature up to the present time is the work of Bachmetjew (1901). He summarized the work of his predecessors, performed numerous experiments and formulated conclusions regarding insect temperatures and cold resistance in insects. He used the thermocouple to measure the temperatures of insects and to record freezing points. He emphasized the time rate of cooling or the "Abkühlings geschwindigskeit" as influencing the vital tempera-

ture minimum, or the lowest temperature at which insects could survive. He also correlated the amount of "sap" present with the freezing point. This term is not quite equivalent to moisture for it represents the difference in weight between a normal insect and a desiccated one. That the weight loss may not be entirely due to water was recognized by Bachmetjew (1899). The size and structure of the cell contents was also recognized by Bachmetjew as correlated with the freezing point. There is one conclusion that Bachmetjew makes with regard to his vital temperature minimum that is difficult to understand. The reaching of the undercooling point for the second time, according to this author, determines death. The undercooling point rather than the freezing point is considered as the critical point. With regard to death occurring at the time of reaching this undercooling point the second time, the data of this author admit of more than one interpretation. About 27 per cent of his results disagree with his conclusion.

Bachmetjew's contributions to the subject of insect freezing can be summed up as follows: (1) the time rate of cooling determines the undercooling point and hence the critical point; the more rapid the cooling the higher the undercooling point; (2) the per cent of "sap" is inversely proportional to the freezing point; (3) the point of death is reached when the insect reaches the undercooling temperature a second time. The lowest undercooling point that was obtained by this author was −15.7°R.

Gueylard and Portier (1916) found that the survival of *Cossus* and *Carpocapsa* on exposure to low temperatures depended upon the season of the year. In winter these larvae were able to survive −20°C. but were killed by that temperature in the spring. In a later paper Duval and Portier (1921) make further observations on freezing points and emphasize further their periodicity. Another contribution made by these authors is the concept of a secondary freezing point. The first freezing point represents the freezing of body fluid while a lower freezing point of the same tissue represents the freezing of the cell substance itself.

Knight (1922) was able to demonstrate a marked periodicity in the freezing point of the Pentatomid, *Perillus bioculatus*. In the fall this bug gained hardiness and in the spring lost it. Knight considered that the freezing point as demonstrated by the thermocouple method was colloidal in nature. Repeated freezing of the same bug brought the freezing and undercooling points nearer and nearer together, with each successive freezing. This action parallels the setting and melting of gelatine and other colloids where the past history influences present behavior.

Pirsch (1923) in a study of the individual temperatures of honey bees found the freezing point was about −1°C. He tried three bees only as his paper dealt chiefly with other phases of the problem of insect temperatures.

Carter (1925) studied the freezing and undercooling points of the bean weevil *Mylabris obtectus*. He found that the insect when uninjured by piercing with the thermocouple was able to withstand lower temperatures than a pierced insect. He found no correlation between the time rate of cooling and the freezing or the undercooling points. The weevils showed no periodicity during the time studied. Representatives of the stored-products pests that would not be expected to show hardening were chosen for his work in order to simplify the problem.

The relation of water content to the freezing point, cold endurance, and hiber-

nation has been suggested by several authors but definitely worked out by comparatively few. Bachmetjew (1899) emphasized the relation between "sap content" and freezing and undercooling points. The work of Tower (1906, 1910) while open to question in some respects is, however, suggestive. The low water content of hibernating forms is emphasized. Breitenbecher (1910) associated with Tower found that he could bring potato beetles out of hibernation by watering the soil in which they were dormant. Bodine (1921, 1923) has found that hibernating grasshoppers possess a low rate of respiration accompanied by a low moisture content. With the breakup of hibernation the water relations are readjusted to a higher level. Hibernation is essentially a rejuvenating process from the standpoint of basal metabolism. Fink (1925) states that hibernating animals have a low respiratory quotient. The breaking up of hibernation in the coddling moth by repeated soakings of the hibernating individuals was reported by Townsend (1924) at the fifth Washington Meeting of the American Association for the Advancement of Science.

Bottazzi and Bergami (1924) reported an irreversible precipitation occurring in ox blood serum when it was cooled to −25°C. They were studying the action of low temperatures upon fluid colloidal systems. Perhaps the most comprehensive work on the relation of water to metabolism is that of Babcock (1912). He studied metabolic water in both plants and animals, and states that during hibernation metabolic water is the source from which animals draw their necessary supplies. The amount of water in hibernating animals is lower than that in non-hibernating animals.

The measurement of the cold resistance of insects has been dependent upon the measurement of temperature itself and upon the applications of methods of temperature measurement to insect material. The invention of the thermometer in 1714 by Fahrenheit, its perfection by Réaumur, together with the interest in measuring temperatures at that period furthered the study of insect physiology. But there is another method of measuring temperatures, namely the thermo-electric method. Volta in 1801 found that an electric current was set up at the junction of two unlike metals. In 1822 Seebeck, using the newly invented instrument, the galvanometer, measured the E.M.F. set up at junctions of unlike substances and correlated these measurements with temperature change. As early as 1831, Nobili and Melloni were recording the temperatures of insects and other small animals by means of the thermocouple.

III. ORIGINAL EXPERIMENTAL RESULTS

The work of the present writer has dealt with the ability of insects to survive temperatures lower than 0°C. The cold resistance was measured by the freezing and by the undercooling points. By freezing is meant actual crystallization of a given body fluid or tissue accompanied by the giving off of heat. By the undercooling point is meant the limiting temperature below the freezing point of a fluid, to which it can be cooled without freezing.

With the thermo-electric method the freezing and the undercooling points of three groups of insects were taken throughout their normal annual cycle. These ecological groups were, (1) the oak borers, normally exposed to temperature extremes; (2) the aquatic insects never exposed to a temperature lower than 0°C., and (3) stored-products pests, represent-

ing, supposedly, a tropical or sub-tropical group.

With the oak borers the freezing and the undercooling points were periodic and varied with the seasons. The lowest freezing and undercooling occurred in winter; the highest in summer; with fall and spring determinations intermediate. A marked correlation between the environmental temperature and the insect freezing and undercooling was formed. The species used in this study were larvae of *Synchroa punctata* Neum., *Dendroides canadensis* Lec., *Elater* sp., *Melanotus* sp., *Chrysobothris femorata*, *Romaleum rufulum* Hald., *Elaphidion mucronotatum* Fab. *Leptura nitens* Forst., *Arhopalus fulminans* Fab., *Xylotrechus colonus*, Fab., *Graphisurus fasciatus* Deg., and the adult of *Nyctobates fasciatus* Deg.

A series of freezing and undercooling points of aquatic insects was also made. The genera used were *Enallagma*, *Ischnura*, *Gomphus*, and *Sympetrum* among the Odonata; *Leptocella*, *Phryganea*, and *Neuronia* among the Trichoptera; *Buenoa*, *Belostoma* and *Notonecta* among the Hemiptera; *Haliplus*, *Cybister*, *Coptotomas* and *Dytiscus* among the Coleoptera. Nymphs of the Odonata, larvae of Trichoptera, adults of the Hemiptera and adults of the Coleoptera were used. Determinations were made in February, May, July and September. There appeared to be no periodicity in these insects. There also seemed to be no significant difference between different species, different orders or different stages of development. The mean undercooling of all aquatic insects was 1.52 ± 0.3, the mean freezing 0.57 ± 0.03.

The insects infesting stored products exhibited no apparent periodicity but were more variable in both undercooling and freezing than the aquatic group. Three species, *Tribolium confusum*, Duval, *Sitophilus granarius* Linn., and *Pyralis farmalis* Linn. were studied with the following results:

INSECT	STAGE	NUMBER DETERMINED	MAXIMUM	MINIMUM	AVERAGE
Undercooling					
Tribolium confusum Duval.....	Adult	200	−6	−1.5	−4.5
Tribolium confusum Duval.....	Larvae	200	−8	−5	−5.6
Sitophilus granarius Linn.....	Adult	200	−14	−2.2	−6
Pyralis farmalis Linn.....	Larvae	500	−7	−4	−6
Freezing					
T. confusum.....	Adult	200	−4.6	−0.5	−2
T. confusum.....	Larvae	200	−8	−7.1	−3.6
S. granarius Linn...	Adult	200	−8	−1.4	−2.4
P. farmalis.....	Larvae	500	−7	−4	−6

The mode of undercooling with *Sitophilis granarius* was −4, of freezing −2. Thus both the mode of undercooling and of freezing differ from the mean. The determinations on this species indicate a highly variable population as regards cold resistance.

Although the oak borer group appears essentially periodic as regards resistance to low temperatures it is possible to alter this character by exposure to suitable temperatures and humidities. Exposure of insects to low temperatures in the summer will start the hardening process. Similarly exposure to high temperatures in the winter time will cause loss of hardiness. The results of these experiments would indicate that the freezing point and undercooling is not itself essentially periodic but is a response to a temperature condition that is periodic. Thus

in northern climates the succession of seasons is essentially periodic.

Cold hardiness can be produced experimentally (1) by exposure to low temperature or (2) by dehydration.

Conditions associated with low freezing and undercooling temperatures were studied. The most pronounced feature was found to be the low moisture content. The insects in fully hardened condition have a low moisture content, in non-hardy condition a high moisture content. Periodicity was exhibited in the moisture content. That of *Synchra Punctata* varied from 31.1 per cent in February to 54 per cent in August. With *Dendroides* the variation in moisture content was more marked, from 57.4 per cent to 73.5 per cent. Larvae were baked for four hours at 50°C.

Some experiments were tried in order to determine the nature of freezing. Repeated or multiple freezings were taken on the same insect or tissue. These freezings and undercoolings so taken remained constant and exhibited no hysteresis. Samples of blood taken from the aortae showed definite crystals. Transparent larvae also were seen to have crystals within at the time the freezing point was recorded. The process of freezing in this group was interpreted as crystalloidal. The first or primary freezing point is the freezing point of the blood.

It was found that when the oak borers were in winter condition they could survive freezing. However, on lowering the temperature still further a second undercooling point was found and a second freezing. This secondary freezing point was always fatal. For the oak borer group it was near −40°C. The tissue freezing was not definitely isolated but experiments pointed to the possibility of the tissue being either fat within the cells or nervous tissue.

The problem of survival of insects at low temperatures was studied in considerable detail with special reference to temperatures below 0°C. It was found (1) that insects not fully hardened were killed when the primary freezing point was reached; (2) in fully hardened insects the primary freezing point was not fatal but there occurred a secondary freezing point that was. Experiments were run to determine the relationship between the freezing point and survival of insects when exposed to low temperatures for as long as twelve hours. It was found that insects with high freezing points were never able to withstand long exposure to low temperatures. However, insects with low freezing points could be killed by long exposure when a short exposure would not be fatal.

With insects not in fully hardened condition the absolute minimum fatal temperature or the lowest at which insects can survive can be defined as the undercooling point. The "vital temperature minimum" of Bachmetjew thus is the absolute minimum fatal temperature for the oak borers throughout the summer, early fall and late spring. During the remainder of the annual cycle, the limit of undercooling is no longer the absolute minimum fatal temperature but the secondary freezing point or some point lower than the primary undercooling must be sought. The secondary freezing point represents the freezing of some tissue other than the blood. One experiment was tried to obtain the freezing point of the nervous tissue. The central nervous systems of fifty larvae were dissected out, placed in a small tube and frozen. The undercooling point recorded was −48°C., the freezing point −45°C.

IV. SUMMARY

Due in part to demand for cold hardy plants and in part to the fact that plant physiology is further developed than

insect physiology, the study of cold resistance in plants has proceeded to a farther stage than the study of cold resistance in insects. From workers in plant physiology we can gain light on certain general physico-chemical problems involved in low temperature studies. The cause of death from low temperature has been considered, (1) as due to direct mechanical injury, (2) water loss through changes in permeability, and (3) precipitation of proteins or other irreversible chemical effect. The development of cold hardiness through slow growth, dehydration, or exposure to low temperatures showed that cold resistance is a dynamic rather than a static condition. Finally, the most recent work on plants has emphasized certain chemical and physical conditions of the plant tissues to be associated with cold resistance. These are low water content, efficient hydrophyllic colloids, and proteins not easily precipitated by low temperature.

The study of survival of insects at low temperatures has gone through (1) the observation stage, (2) the qualitative experimental, and is now entering the third stage, the quantitative. Studies on hibernation, on individual insect temperatures, and on heat regulation in insects, have all contributed to the general problem of freezing and survival of insects at low temperatures. Determinations for some insects have thus far been made as to the intensity of low temperatures they can survive, and whether or not they can withstand ice formation in their tissues. Aside from the finding that low water content is associated with cold resistance there yet remain to be discovered the physico-chemical factors associated with or causing cold hardiness in insects.

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RENNER'S STUDIES ON THE GENETICS OF OENOTHERA

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THERE is only one group among the higher animals and plants that has persistently failed to give genetic results that can easily be interpreted by means of the generally applicable principles. The Evening Primrose (*Oenothera*) has been studied for thirty years, first by de Vries and more recently by a number of other workers; but the results obtained are still quite anomalous as compared with what is known of any other intensively studied organism. The cytological work of Miss Lutz, Gates, Stomps, Boedijn and others has now shown that many of the results are due to the occurrence of triploid, tetraploid, and "trisomic" (2n + 1) types; but apart from variations in chromosome number there remains a mass of puzzling data as to the behavior of the 14-chromosome species and "mutant" races.

Oenothera Lamarckiana was long ago shown by de Vries to produce regularly about 2 per cent of "mutant" offspring. About three fourths of these can now be identified as due to extra chromosomes; the remainder appear to be due to heterozygosis in the parent. But if *Lamarckiana* is regularly heterozygous, why does it not produce a still higher percentage of new types—at least 25 per cent—among its offspring? When *Lamarckiana* is crossed to other species of *Oenothera*, F_1 usually includes two distinct types, though both parent species breed nearly true—and these "twin hybrids" themselves often breed nearly true. Many species crosses in *Oenothera* give different results according to which species furnishes the egg, which the pollen. Finally, the ratios obtained from various mutant and species crosses in the group are variable and are rarely in accord with simple Mendelian expectations.

These and other remarkable peculiarities of the Evening Primrose have been intensively studied in Germany by Professor Otto Renner, and it is the purpose of the present review to show how Renner's work helps to explain the genetic behavior of *Oenothera*.

The first two papers to be considered (1914, 1917a) deal with the problem of the twin hybrids produced by *Lamarckiana*. Renner found that when *Lamarckiana* is self-fertilized, about half the seeds formed are incapable of germination. But when *Lamarckiana* is fertilized by *biennis* or *muricata* (crosses which result in twin hybrids) practically all the seed is viable. Renner therefore assumed that *Lamarckiana* is heterozygous for two gene-complexes, neither of which is viable when homozygous. One of these, called *gaudens*, produces the twin known as *laeta;* the other, known as *velans*, produces the twin *velutina*. *Lamarckiana* is then *gaudens-velans;* the inviable seeds are *gaudens-gaudens* and *velans-velans*. The hypothesis accounts for several other facts, such as that *Lamarckiana* may be

reconstituted by crossing *laeta* and *velutina*. Renner further suggested that some of the mutant types were due to exchange of materials between the *gaudens* and *velans* complexes.

Genetic studies (1917b, 1917c, 1918a) showed that the wild species *biennis*, *suaveolens*, and *muricata* are likewise complex heterozygotes—as was also clear from the earlier results of de Vries. Renner has given special names to the haploid gene-complexes of these species and of *Hookeri*, as follows (*Lamarckiana* is included for completeness):

biennis = *albicans*, *rubens* ♀ — *rubens* ♂
Lamarckiana = *velans*, *gaudens* ♀ — *velans*, *gaudens* ♂
muricata = *rigens* (*curvans*) ♀ — *curvans* ♂
suaveolens = *albicans*, *flavens* ♀ — *flavens* ♂
Hookeri = ^{h}*Hookeri* ♀ — ^{h}*Hookeri* ♂

That is to say, *biennis* produces *albicans* and *rubens* eggs, but only *rubens* pollen; *muricata* produces mostly *rigens* eggs, but a few *curvans*; *Hookeri* produces only ^{h}*Hookeri* (read haplo-Hookeri) eggs and pollen. *Biennis* breeds true because *rubens-rubens* dies, *muricata* because *curvans-curvans* dies, and *suaveolens* because *flavens-flavens* dies. *Hookeri* breeds true because it is homozygous: practically all its seeds are capable of germination, and it gives uniform progenies when selfed.

But why do *biennis*, *muricata*, and *suaveolens* produce only one kind of pollen? This problem was attacked by a microscopic study of the pollen grains themselves (1919a, 1919b). In *Hookeri* the pollen grains were found to be uniform in appearance, and practically all were well filled and capable of germination. In all the other species roughly half of the grains were small and empty—quite obviously not capable of germination. These can not be the grains that carry the gene-complexes (*albicans*, *rigens*) that are absent in the functional pollen, since such bad grains are present in *Lamarckiana*, where both complexes give functional pollen. I shall discuss the bad grains later. In *biennis*, *muricata*, and *suaveolens* the fully formed and well filled pollen grains were themselves found to be of two kinds, equally numerous. One kind was larger than the other, and staining with iodine showed that the starch grains in the larger kind were more spindle-shaped, those in the smaller more spherical. Only the large grains with spindle-shaped starch grains germinated *in vitro*, and when the pollen was placed on stigmas, sections of the styles showed only spindle-shaped starch grains in the pollen tubes. These grains then represent *curvans*, *rubens*, and *flavens;* the round starch grains are present in *albicans* and *rigens* pollen. These conclusions were fully verified by a study of the pollen grains of hybrids of known constitution. The most intensively studied is *curvi-velutina*, at first called *gracilis* (*Lamarckiana* × *muricata*) = *velans-curvans*. The two kinds of pollen produced agreed in size with the grains of *Lamarckiana* (distinctly larger than those of *muricata*) and with the *curvans* grains of *muricata*. Their starch grains also differed in shape, those of *velans* being more spindle-shaped. Studies of the pollen tubes in flowers fertilized by this hybrid showed that the *velans* grew faster than the *curvans*. The genetic results thus become intelligible; for in the short-styled *muricata* and *biennis* some seeds are fertilized by the *curvans* pollen of this hybrid, while in the long-styled *Lamarckiana velans* alone reaches the eggs. In crosses to short-styled plants *velans* fertilizes more eggs than *curvans*, but if competition is decreased by the use of a small amount of pollen, the percentage of *curvans* rises. We have here, then, an important cause of variable and atypical ratios from

Oenothera hybrids. More important still, the method is available for a direct study of non-functional or poorly functional pollen, so that one no longer feels that assumptions as to the nature of the pollen grains simply beg the question.

The eggs of heterozygotes are also sometimes produced in unequal numbers—notably in the case of *muricata*, which only rarely produces *curvans* eggs. The mechanism at work here has been studied by Renner (1921b). Each ovule of *Oenothera* contains a single diploid megaspore-mother-cell. This cell undergoes two maturation divisions, giving rise to four haploid megaspores. These are separate cells (not merely nuclei in a single cell, as in some seed plants), and are arranged in a row. The two upper megaspores, nearest the micropyle, are sister cells—i.e., they come from one of the two cells produced by the first maturation division; the two lower megaspores, nearest the chalaza, come from the other product of the first maturation division. If, as seems probable, the first division is the reduction division, the two upper cells are alike in genetic constitution, and are different from the two lower cells. In *Hookeri* Renner found that the uppermost cell regularly developed into the embryo sack, the three lower cells all degenerating. It is evident that in this case, where all the megaspores are genetically alike, the upper cell has an advantage due to its position alone, and as a result of that advantage it succeeds in growing at the expense of its companions, until it comes to fill the entire space within the nucellus. In the ovules studied, the same result was found for *Lamarckiana*, as was to be expected; for *Lamarckiana* produces both *velans* and *gaudens* eggs, often in nearly equal numbers. But in *muricata* the uppermost cell gave rise to the embryo sack in only about half of the ovules. In the other half the lowermost cell grew faster than the other three, and ultimately came to be the only one present. Evidently in half the ovules the *rigens* complex is segregated to the upper cells, and the usual course of events follows. In the other half of the ovules, *curvans* goes to the upper cells, *rigens* to the lower; and in this case the *rigens* cells have a sufficient inherent advantage over the *curvans* so that they usually succeed in overcoming the disadvantages of their position. The genetic results show that the various complexes can be roughly classified according to their "strength" in such competition between megaspores. *Curvans* is always "weak," *velans* is always "strong." *Rubens* never succeeds in competition with *velans*, is usually unsuccessful against *albicans*, but never fails against *curvans*. It is clear that these results can not be explained by assuming the presence of egg lethals; but the competition interpretation does work out consistently.

Another complication cleared up by Renner (1922, 1924) is the behavior of the chloroplasts in *Oenothera* hybrids. It was shown by de Vries and others that species hybrids in this group sometimes are white or pale green, or are mosaics of green and pale regions. *Hookeri* ♀ × *Lamarckiana* ♂ gives two kinds of hybrids, *[h]Hookeri-gaudens* and *[h]Hookeri-velans*, which are both normal green in color. The reciprocal cross, *Lamarckiana* ♀ × *Hookeri* ♂, gives a *[h]Hookeri-gaudens* like the preceding one; but the *[h]Hookeri-velans* is either pale green or mottled pale green and dark green. Renner shows that this result is explicable on the assumption that the plastids of *Lamarckiana* are not able to develop their normal amount (or kind) of chlorophyll in the presence of *[h]Hookeri-*

velans (or *ʰHookeri-ʰHookeri*) nuclei. Some of the hybrids, however, obtain a few plastids from the *Hookeri* pollen tubes, and these develop into the occasional dark green patches. The hypothesis was tested by many crosses. The *ʰHookeri-gaudens* sisters of the mosaics, when selfed, give rise to homozygous *Hookeri* plants, which are pale green, without any patches. But if the same *ʰHookeri-gaudens* is fertilized by pollen from *Hookeri*, some of the resulting homozygous *Hookeri* have dark green patches, evidently because *Hookeri* plastids have been introduced by the pollen. In certain combinations involving other species both of the reciprocals are mosaics. *Rubens-curvans*, for example, is white when the plastids come from *biennis*, green when they come from *muricata*. The F_1 plants are white with a few green patches when *biennis* is the mother, green with pale spots when *muricata* is the mother. Such mottled plants often produce branches that are entirely of the dark green color characteristic of the paternal plastids; in such cases the flowers on these branches behave genetically also as though they had only paternally derived plastids. In general, the results make it clear that the development of chlorophyll depends on the constitution of the nuclei and also on that of the plastids themselves. The plastids of each species have characteristic properties, which are transmitted as such and are not at all affected by the nuclear constitution. A plant may have *muricata* plastids and transmit them to its offspring, even though its nuclei do not contain either *rigens* or *curvans*. These results serve to explain the occurrence of white and pale green inviable seedlings, and to clear up another cause of differences between reciprocal hybrids—besides being in themselves perhaps the most instructive cases of plastid inheritance yet recorded.

Renner has consistently aimed at the analysis of the gene-complexes of *Oenothera* into their component Mendelian units. His most recent paper (1925) gives a summary of the results so far obtained in this direction. As early as 1917 he suggested that the complexes do sometimes interchange materials, and that many of the mutant types of de Vries and others are due to such interchanges. *Gaudens*, for example, carries a recessive gene for dwarfness, and this occasionally goes over to *velans*, giving a *velans*-plus-dwarfness or "*nanovelans*" complex. There results the familiar mutant type *nanella* = *gaudens-nanovelans*. The pale flowered type *sulfurea* of *biennis* is produced in a similar way; and it is probable that many of the other types of *Lamarckiana* (such as *deserens*, *decipiens*, and *blandina*) are also due to exchanges of material between opposing complexes.

Renner has especially studied the various hybrids of the five species that he has worked with. Practically all the possible combinations of the eight primary complexes have been obtained, and their offspring studied. (*Albicans* and *rigens* never function in pollen, and therefore can not be obtained together. *Rubens* and *gaudens* have a common zygote lethal, so that *rubens-gaudens* dies.) Some of these (e.g., *curvans-flavens*, *rigens-velans*, *ʰHookeri-rigens*) give a distinctly higher percentage of new combinations than do the original species. The data do not as yet suffice to show in detail how the various complexes are related in terms of genes; but several results are clear, and there are a large number of other partial analyses. I shall here only point out a few of the more striking results. The *curvans* complex is shown to carry two distinct and separable zygote lethals.

The zygote lethal of *flavens* may be replaced by a viable allelomorph from *rubens*, *rigens*, or *gaudens*, so that plants homozygous for practically the whole *flavens* complex may be obtained and studied. The gene R, for red nerves, acts as a zygote lethal (as shown by Heribert-Nilsson). It occurs in some races of *Lamarckiana*, and is there independent of the *velans-gaudens* complexes in inheritance. It is sometimes present in *rigens*, and is always present in *rubens* but never in *albicans*—i.e., in *biennis* it is completely linked to the rest of the genes composing the two complexes. In *curvans-velans*, when R is present and was received from the *Lamarckiana* parent, it is completely linked to *velans*—though in *Lamarckiana* it was independent of *velans*.

Renner discusses three possible interpretations of the interchanging of elements between complexes.

1. Linkage, due to the genes concerned all being carried in the same chromosome pair. This interpretaton is accepted by Renner as accounting for at least part of the results—i.e., some of the genes concerned probably do show linkage of the ordinary type. But an attempt to account for all the results on this basis meets with difficulties—chiefly in that at least three (perhaps four) loci may be completely linked in some combinations, whereas in others they may be completely independent. The chromosome would therefore have to be extremely long (as measured by crossing over), and would also have to be subject to very striking variations in crossing over.

2. The genes concerned are really independent in inheritance, but nearly all the new combinations of them are inviable. It seems certain that many of the new combinations are inviable, and the empty pollen grains referred to above are probably mostly to be attributed to this cause, as are also the numerous inviable female gametophytes. But it is easy to show that there is not enough elimination of gametes and zygotes to account for the number of different genes for which the plants are heterozygous. It follows that the parental combinations are produced in larger numbers than are most of the new combinations.

3. Chromosome linkage. The cytological observations of Cleland suggest that the chromosomes are not segregated at random at the reduction division; and Renner is inclined to think that in this direction is to be sought a still further special complication of the *Oenothera* situation. He even outlines a tentative arrangement of the genes and groups of genes separated from the various complexes among five of the available seven pairs of chromosomes. This arrangement is intended only as a working hypothesis; but it should be possible to test it cytologically and by the use of trisomic types.

In the present review I have only attempted to give the general results and a few special examples. In the original papers (especially 1919b and 1925) the reader will find an astonishingly large amount of data, and abundant evidence that Renner has spared no pains to put his hypotheses to every available test.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

A PHILOSOPHICAL INTERPRETATION OF NATURE

Being a review of *Science and the Modern World: Lowell Lectures*, 1925, by Alfred North Whitehead, Fellow of Trinity College in the University of Cambridge and Professor of Philosophy in Harvard University. New York (Macmillan), 1925. $4.00.

By Lawrence J. Henderson, Harvard University

This book of Lowell lectures, in the author's phrase, "embodies a study of some aspects of Western culture during the past three centuries, in so far as it has been influenced by the development of science." It describes an epoch during which, on the whole, older interpretations of life, of the world, and of nature have steadily lost ground to materialism and to a mechanistic philosophy based upon physics. The main ideas which have guided this continuous evolution of modern thought are developed in broad outline, from the standpoint of the specialist in theoretical physics, but with an ever present sense that nothing can be more important than a dominant philosophy. Such, in substance, is Whitehead's modest description of a work which is also an important and original contribution to philosophical thought, which may possibly be destined to revolutionize our interpretation of nature, and which, at any rate, goes far to replace materialism by a philosophy of organism. The present state of science and of thought, and the search for a way out of present difficulties through recognition of organization as the most concrete reality of nature, make up the real subject matter of this book. For this reason biologists and naturalists will find here the clear expression that they have long needed of ideas which they themselves can neither escape nor, without aid from physics and philosophy, sharply define.

The book opens with a discussion of the fascinating and difficult problem of the origins of the modern scientific mind. "The most intimate change in outlook which the human race had yet encountered" commenced quietly with the appearance of a new interest, or a new intensity of interest, in the bearing of irreducible, stubborn facts upon generalizations. It was carried forward because men who were fired by a strong, unyielding faith that everything exemplifies general principles, and that these can be

known, also became "apt for the state of imaginative muddled suspense which precedes successful inductive generalization."

This phrase must not be passed by without remark, for I feel sure that no experienced investigator can read it and remain unmoved. Its self-evident truth shows how far the problem of scientific method is psychological, and, to me at least, it seems a well nigh perfect statement of the *differentia* of the man of science at work.

From another standpoint Whitehead sees the beginning of modern science as an anti-intellectualist movement arising from the perception that nature is more subtle than the human reason. This is a reaction against the rationalism of mediaeval theology, yet modern faith in the possibility of science remains as an unconscious derivative therefrom. Again, modern science could not be what it is without a vision of the order of nature as akin to the remorseless inevitableness of Fate in Greek tragedy.

Another almost independent ingredient of modern science is noted in the rise of Naturalism in the later Middle Ages, especially in decorative sculpture. This precedes and is the source of the scientific interest in objects for their own sake.

Once established, modern science soon experienced the formative influence of mathematics. The Arabic notation, algebra, logarithms, analytical geometry, and the infinitesimal calculus were the necessary instruments of the great achievements of the incomparable seventeenth century. Its men of genius have stamped physics with the mark of mathematics, and physics determines the character of the century. In Whitehead's opinion "a brief, and sufficiently accurate, description of the intellectual life of the European races during the succeeding two centuries and a quarter, up to our own times, is that they have been living upon the accumulated capital of ideas provided for them by the genius of the seventeenth century." No doubt an exception to this statement is to be made in favor of the idea of evolution. Most of these ideas we owe to that development, perhaps the greatest in the history of the intellect, which began with Galileo and ended with Newton, including also the labors of Descartes and Huyghens. It is all summed up in Newton's *Principia*.

This development provided posterity with a blank form of a universe, which remained to be filled up. It produced the concepts of inertia, of mass, of an isolated system, of conservation and of force; and it led to the secure foundation of the mechanistic theory of nature, "which has reigned supreme ever since the seventeenth century. It is the orthodox creed of physical science. Furthermore, the creed justified itself by the pragmatic test. It worked. Physicists took no more interest in philosophy. . . . . But the difficulties of this theory of materialistic mechanism very soon became apparent. The history of thought in the eighteenth and nineteenth centuries is governed by the fact that the world had got hold of a general idea which it could neither live with nor live without."

The difficulty is most easily seen in the inconsistency of our mechanistic philosophy, which enthrones physical causation as supreme, with our political and social judgments, which always imply final causes. As Whitehead remarks, "it is not popular to dwell on the absolute contradiction here involved." This leads to the problem of freedom and to Mill's famous doctrine, which is promptly dismissed with the scant courtesy which it deserves. Thus we reach a position which has often been reached before, but which

has always seemed a cul-de-sac. Countless biologists during the last half century have found themselves in the ridiculous situation, from which there was no escape, of paying lip-service to the mechanistic theory which was never of the slightest usefulness or relevancy in their researches. The difficulty has always been that the mechanistic theory was known to work; in fact it often worked quite as well in bio-physics and biochemistry as elsewhere. Yet in morphology, cytology, genetics, ecology, and similar sciences it has been mainly irrelevant.

Meantime, however, a change has come over physics. As a result of the rise of modern atomism, of the theory of relativity and of the quantum theory, the solid foundations have melted away, and it is not yet possible to judge of the new foundations which must some day replace them. What then "is the sense of talking about a mechanical explanation when you do not know what you mean by mechanics." No one who sees clearly can fail to perceive that the breaking up of the classical philosophy of physics must infallibly release biology from a bondage which has in the past done much good and much harm. The old sanctions, in truth, no longer hold; but, as always, men who have formed the habit of respectful obedience to the law do not know when they have been set free. The news must be spread, and other sanctions, better suited to its needs, must be set up by an independent biology; only there must be no return to vitalism.

At the very moment when the old concepts of science—time and space, matter and motion, energy, mechanism and many others—have lost their intelligibility, physiology, following the path which Claude Bernard mapped out, has finally attained a position of independence. This result, though indirectly favored in many respects by the orthodox scientific philosophy of the past half century, has also been retarded by it. In particular, the doctrine of organism has had to win through on its merits. A relatively concrete interpretation of nature, it has met persistent opposition from "the intolerant use of abstractions [which] is the major vice of the intellect."

In the concept of organism, Whitehead believes that he has found a means to construct a philosophy which shall replace mechanism. Consider, for instance, the quantum theory and the atom. The electron is a vibratory entity; in his view it may probably be regarded as an entity *constituted by* the vibrations. Hence its path in space can only be represented by a series of discrete, discontinuous positions, and, on this view, it could not even exist except as a periodic system. So far as we know, its existence at an instant is no more conceivable than the existence at an instant of a musical note. The significant thing about it is pattern, not substance; its essence seems to be its characteristic pattern; in short, it is an organism. (This, of course, implies a definition.) No doubt if we are ever successfully to think of electrons in this manner, we must overcome some of our deeply ingrained habits of thinking. Especially we must get rid of the most fundamental of all our scientific concepts, that nature is made of matter "which has the property of simple location in space and time" and "that the world is a succession of instantaneous configurations of matter."

Here it should be pointed out that such a task, immensely difficult in itself, will be made still more difficult because the classical methods of physics will probably long remain the most economical for disposing of the vast stores of accumulated

knowledge. Also there is almost certainly a psychological predisposition in favor of classical materialism, which, I think, makes it seem the most 'reasonable' philosophy to 'reasonable' men. On this account, and because of its marvelous power, I cannot escape the conviction which, though not expressed, is probably also Whitehead's view, that, through all changes of philosophical opinion concerning its truth, the classical theory is likely forever to remain in use as one of the indispensable means of thinking about physical phenomena.

But in spite of its efficiency, in spite of its acceptability, Whitehead believes that, even from the standpoint of naive realism, materialism "is quite unbelievable. This conception of the universe is surely framed in terms of high abstractions and . . . . we have mistaken our abstractions for concrete realities." The criticism seems to be that scientific materialism involves, and must involve, the error which may be called "the fallacy of misplaced concreteness." Therefore the interpretation of nature must be recast and founded upon the concept of organism. For such a philosophy, process is the concrete fact; organism itself is process; and nature is an organic structure of evolving processes. "Nature exhibits itself as exemplifying a philosophy of the evolution of organisms subject to determinate conditions." Here an organism is correlative with what is a bit of matter from the standpoint of materialism.

His doctrine, Whitehead calls the theory of organic mechanism. It aims to be an objectivist philosophy, and to take account at once of the needs of natural science and of the nature of our concrete experiences. In spite of its difficulty, it is a form of naive realism and is rooted in naive experience. In this respect his reference to poetry is significant, and, I believe, reassuring. In particular, the theory thus emphasizes the final elimination of the doctrine of primary and secondary qualities, which has always been one of the scandals of classical materialism.

Nature, being evolutionary, is characterised by emergent "*events*." The event is a transitory unity possessing value; "it is the ultimate unit of natural occurrence;" but it is no independent entity, for this, on the organic theory, is impossible. Every event is (prehensively) related to all other events, and these relationships are internal, that is to say constitutive.

The concrete enduring entities of the world are organisms. In them the parts, even though themselves organisms, are influenced by the plan of the whole. This is true both within and below the biological sphere. "In the case of an animal, the mental stages enter into the plan of the total organism and thus modify the plans of the successive subordinate organisms until the ultimate smallest organisms, such as electrons, are reached. Thus an electron within a living body is different from an electron outside it, by reason of the plan of the body."

But the pattern of an organism does not changelessly endure. There is a cyclical, rhythmic and recurrent aspect to all endurance which may be expressed by the word "reiteration." Perhaps the harmony or stable pattern of vibratory periods among its constituents is, at the very bottom of the organic scale, in the proton and the electron, the clue to the stability of the organism, and also to adaptation to the environment.

To continue the analysis would lead deep into the fields of metaphysics and of the modern theory of atomic structure, for this work includes the sketch of a large fragment of a new metaphysical system, founded on the most recent

scientific thought and speculation. It is a system novel in itself, and peculiarly important because informed by the knowledge and experience of a professional mathematician and physicist. Since Leibniz there has been no similar approach to philosophy. Perhaps for this reason there are in Whitehead's speculations certain affinities with Leibniz. It is not a question, however, of a common philosophical position. On the other hand, there may be found in Lachelier's essay on Induction, and perhaps in the writings of Cournot, views on one philosophical question which are very close to those here set forth. It is also not uninteresting to note the contrast with Fechner's "Cosmorganic" hypothesis, which no doubt developed from a vague perception of the difficulties which Whitehead has clearly analyzed. But, in spite of physical origins, and the pervasive physical and mathematical coloring with which this work is imbued, the main affinities of Whitehead's central hypothesis are biological. The background that one wants in order to have a setting, within which Whitehead's theory may be clearly seen and closely scrutinized, with no sense of discomfort or constraint, is perhaps best afforded by the biological works of Aristotle and by the theoretical physiology of Claude Bernard. The writings of J. S. Haldane present a related hypothesis, and theoretical ecology also involves similar concepts.

The book contains, among other things, an excellent condensed statement of the larger features of the history of modern science. Some of the historical judgments are of great importance, and there are frequent shrewd explanations of what has really gone on beneath the surface. There are also several chapters devoted to the discussion of philosophical problems which, though important from the standpoint adopted by the author, bear but slightly upon biology. Many references will be found to general history and to literature.

Partly because of the lecture form, and also on account of the all inclusive subject matter, the book is somewhat disorderly. But it is beautifully written and abounds in profound, wise, and witty remarks, a few of which have been quoted in this review.

No doubt the real cause of a certain lack of unity in the exposition lies deeper. The author is, manifestly, still engaged in working out his theories into what promises to become a complete philosophical system of "organic mechanism." He has now provisionally consolidated the positions to which he has thus far attained. But he is still pressing forward, and, until the enterprise has been completed, there can be neither time nor opportunity for a formal and exhaustive discussion.

It is impossible to foretell what the fate of this system is to be. I can only say that I seem dimly to perceive in it, for the first time, the possibility of escape from the difficulties that have produced the conflicts between mechanism and vitalism, and between freedom and determinism. But here hope has been so long deferred that it is natural to be a sceptic. Meanwhile this sketch of a new philosophy may well suffice to restore and to expand our vision of the scope of biology. Like every other human enterprise, biology needs to be understood as something which is valuable in itself and which is not secondary to other enterprises, but the equal of any. As an "event," in Whitehead's sense, biology acquires just this kind of value. But it also now appears as the science which approaches nearest to the concrete enduring realities of the world. Thus, to the biologist, this book is so important that we may not yet

venture to estimate its importance. One thing is certain; for the first time since modern science gained control of modern thought, a philosophical interpretation of nature has appeared which is based upon a master's knowledge of physical science, and which assigns to the fact of organization that position in a thoroughly comprehensive scheme of things, to which biologists know that it is entitled.

BRIEF NOTICES

EVOLUTION

SCIENCE, RELIGION AND REALITY.

Chapters by Arthur James, Earl of Balfour: Bronislaw Malinowski; Charles Singer; Antonio Aliotta; Arthur S. Eddington; Joseph Needham; John W. Oman; William Brown; Clement C. J. Webb; William Ralph Inge. *The Macmillan Co.*

$2.50 6 x 8¾; 396 *New York*

This book is a valuable contribution to the discussion of the old problem of the conflict between science and theology. The distinguished contributors are all philosophically minded persons of high technical competence in the fields with which they deal. Dean Inge's concluding chapter is a fine piece of clear thinking. Witness to this statement is borne by the following quotation, which is commended to the attention of American scientists and American theologians equally:

"There are at least three positions between which the Church may make its choice. It may condemn modern astronomy as impious and heretical, as the Inquisitors and the Reformers agreed in doing. Luther denounced Copernicus as a fool who dared to contradict the Bible, 'an upstart astrologer who dared to set his own authority above that of Holy Scripture.' Melanchthon thought that those who set forth such theories must have no sense of decency; and Calvin asked, 'Who will venture to place the authority of Copernicus above that of Holy Scripture?' The Roman Church has lately condemned the doctrine of evolution in terms not less stringent than these. This is one possible policy. It declares that there can be no truce between science and religion till science has renounced its errors and accepted the authority of the Church.

"A second policy, equally open to the Church, is to admit that these traditional doctrines do not belong to the natural order with which science deals, but to claim that they possess a higher truth, to which science cannot reach. This may be done by regarding these and other dogmas as symbolic of eternal truths, aids to the imagination in forming clear conceptions of revealed truth in a region beyond the compass of our senses. The apologist for tradition who takes this line will not be content to justify the use of symbols. He will point out that science itself is an imaginative construction; that the supposed laws of nature are not derived directly from our observation of the behavior of atoms and molecules; that what are called the assured results of science are the work of the mind upon an abstract view of reality, which neglects the values and qualitative properties of things, and attempts to construct a universe out of mathematics and chemistry. This disparagement of science as incapable of forming any adequate synthesis may be pushed so far as to reach what is called acosmism, the theory which denies the objective existence of the world or universe. The conclusion will then be, that though the dogmas in question

are symbolic, they are much nearer to truth than the scientific laws which pronounce them to be impossible.

"The third policy is to recognise that all theological doctrines which rest upon the geocentric theory must be recast, inasmuch as the results of science are, within their own sphere, unassailable. I do not think I underestimate the seriousness of this step, nor the great difficulties in taking it. But anything, I believe, is better than trying to conceal an open sore which destroys our joy and peace in believing. If we adopt this third policy, we shall be driven to think of God less anthropomorphically, and of heaven as a state rather than a place—a state, too, which is eternal in a deeper sense than that of unending time-succession. But I cannot pursue this subject without transgressing the lines set for writers in this volume.

"If I had any doubts that the religion of Christ can and will weather the storm, or if I had any doubts that it is entirely independent of any false opinions about the nature of the universe, my readers may be certain that I should not have spoken as I have done. If I believed that Christianity stands or falls with a Ptolemaic universe, I should be obliged either to take the painful course of confessing that I have believed and taught all my life a creed which is as outworn as Paganism, or I should do like thousands of others—I should hold my tongue. But I am quite confident that this crisis will be surmounted if the Church has faith and courage, and, above all, the common honesty, to face candidly. Only let us hear no more of clergymen thanking God that theology and science are now reconciled, for unhappily it is not true" (pp. 359–60).

Is it permitted the scientist to thank God that there is at least one theologian who can think straight and clearly, and has courage?

THE ASCENT OF MAN BY MEANS OF NATURAL SELECTION.

By Alfred Machin Longmans, Green and Co.
$2.75 xx + 325 *London and New York*

This book attempts to arrive at a reasonable explanation of the evolution of modern civilized man. It is based in the main on a re-examination and reinterpretation of the works of Darwin and Spencer. Spencer's main contribution to the problem is held to be that human nature (man as he is) can only be explained by the theory of his descent from a long line of savage ancestry. Darwin's theory of natural selection in Machin's opinion serves, as nothing else serves, to explain the fitful, spasmodic and extraordinary progress of the human race.

The book is well written and will be a valuable addition to the shelves of any biological library. Unfortunately it has no index.

EVOLUTION IN THE LIGHT OF MODERN KNOWLEDGE.

A Collective Work. Contributors: F. O. Bower, James H. Jeans, Harold Jeffreys, E. W. MacBride, W. M'Dougall, C. Lloyd Morgan, M. S. Pembrey, A. A. Robb, G. Elliot Smith, Frederick Soddy, A. E. Taylor, W. W. Watts, Rev. J. M. Wilson.
D. Van Nostrand Co.
$7.50 6 x 9; xiv + 528 *New York*

As is to be expected, the contributions of the thirteen different men who write this book are somewhat uneven in quality. Some reach a high standard of popular scientific writing, while others seem somewhat feeble, or biased, or both. What the book attempts to do is to give

an authoritative statement, by representative British scientific men, as to how the doctrine of evolution now stands after the general upheaval of fundamental theories in the last twenty years. The subjects covered are: Cosmogony (Jeans); the evolution of the earth as a planet (Jeffreys); geology (Watts); biology (C. Lloyd Morgan); botany (Bower); zoölogy (MacBride); physiology (Pembrey); anthropology (G. Elliot Smith); mental evolution (M'Dougall); physics and chemistry (Soddy); time and space (Robb); philosophy (Taylor); the religious effect of the idea of evolution (Wilson). Brief bibliographies follow each chapter, and a good working index completes the book. It can be highly recommended as required reading in any general elementary course on evolution.

EVOLUTION, GENETICS AND EUGENICS.

By Horatio Hackett Newman

The University of Chicago Press

$3.50 6¼ x 9¼; xx + 639 *Chicago*

This is a new and extensively revised edition of the author's widely used textbook. It is constructed on the scrapbook plan, being composed largely of excerpts from the writings of the principal authorities in the fields covered. Considerable pedagogical skill is shown in the arrangement of the material in this new edition, there having been some changes from the arrangement in the first edition. The additional material of greatest interest is a chapter dealing with the Scopes trial at Dayton, Tennessee. In reading this one cannot avoid a little of the feeling that perhaps if the general plan of the rest of the book had been strictly adhered to, and extensive quotations made from either H. L. Mencken's newspaper account of the trial at the time, or from the writings on anti-evolutionists of Thomas Henry Huxley—the only professional biologist who ever successfully and admittedly demolished the fundamentalists on their own ground—a more realistic picture of the significance to human thought of the events in Tennessee might have emerged. A short bibliography, an excellent glossary of technical terms, and an adequate index close the volume.

EVOLUTION AND GENETICS.

By Thomas H. Morgan

Princeton University Press

$2.00 5¾ x 8½; ix + 211 *Princeton, N. J.*

This is a revised edition of the author's well-known Vanuxem Lectures for 1915-16, originally entitled "A Critique of the Theory of Evolution." A good deal of new material has been added, and the original four chapters expanded to thirteen. While intended for a lay audience, the main problems of evolutionary biology are discussed with a critical vigor which is as admirable as it is unusual in these days. The last chapter on human inheritance is especially to be commended.

THE DOGMA OF EVOLUTION.

By Louis Trenchard More

Princeton University Press

$3.50 5¼x9½, viii+387 *Princeton, N. J.*

In this volume a physicist criticizes the work of biologists on the problem of organic evolution from a general philosophical standpoint. Some of this criticism is well founded and well sustained and may be read with profit by any biologist. Much of it is mere special pleading in favor of religious mysticism as a system of philosophy. The book seems

certain to be seized upon by fundamentalists as a valuable source of ammunition for their campaign. It lacks an index.

DIE METHODEN DER PHYLOGENETISCHEN (STAMMESGESCHICHTLICHEN) FORSCHUNG (*Handbuch der biologischen Arbeitsmethoden, Lieferung 177*).
By Heinrich Hugo Karny
Urban & Schwarzenberg
12, 60 Marks 7 x 10; 290 *Berlin*

This number of the great Abderhalden Handbook of Biological Technique is strongly recommended to the general biologist. So far as we know, there does not exist in the literature any other book which covers quite the same ground as this in quite so useful a way. What it does is to give a general picture of the philosophy and logic of the methodology of paleontology, as applied to the elucidation of the problem of organic evolution. In doing this it also gives a general picture of what paleontology has accomplished towards the solution of this problem. Some enterprising American publisher might do well to arrange for the translation of this volume, if possible.

GENETICS

EXPERIMENTS IN GENETICS.
By Charles Chamberlain Hurst
The Macmillan Co.
$16.50 7½ x 10½; xxiv + 578 *New York*

This magnificent piece of book making by the Cambridge University Press, collects into one volume the more important papers covering the genetic work of the author during the thirty years from 1894 to 1924. Major Hurst was a real pioneer in genetics, having begun his work on the hybridization of orchids under the inspiration of Darwin's *Fertilisation of Orchids* in 1894, before the dawn of the Mendelian era. Except for the interruption of the War he has been actively engaged in genetic researches from that date to the present time. The papers in this book fall into four general groups. The first, consisting of the first four papers, deals with the orchid work. The next twenty papers report the results of Mendelian experiments with various genera of plants and animals, together with genetic studies of a more statistical character in horses and in man. The next ten papers discuss mainly the problems of the application of the principles of Mendelism to the practical breeding of plants and animals, and also to some extent with eugenics. The last two papers have to do with the author's latest researches on the genetics of the genus *Rosa*. It is a useful service to genetics to have these papers, originally published in widely scattered journals, collected in a single volume for reference.

ÜBER VARIABILITÄT, KORRELATIVE BEZIEHUNGEN UND VERERBUNG DER HAARFEINHEIT BEI SCHAFEN.
(*Bibliotheca Genetica*, Band VII.)
By Walter Spöttel *Gebrüder Borntraeger*
30 Marks 7¼ x 10⅛; iv + 235 and 8 pp. tables *Leipzig*

This extremely thorough and detailed biometric and genetic study of wool deals principally with the following topics: (*a*) the methods of measuring fineness of wool and the biometric treatment of these measurements; (*b*) the fineness of the wool of different races of sheep; (*c*) the correlation between fineness of wool and other morphological and physiological characteristics; (*d*) the inheritance of fineness of wool, in which section the author describes in detail his experimental work

in crossing Mouflon and Somali sheep with Merinos. There is a bibliography covering five pages. Extensive tables of original data are given as an appendix.

OUR PRESENT KNOWLEDGE OF HEREDITY. (*A Series of Lectures Given at the Mayo Foundation and the Universities of Wisconsin, Minnesota, Nebraska, Iowa, and Washington (St. Louis), 1923–1924.*)
W. B. Saunders Co.
$2.50 5½ x 8; 250 pp. *Philadelphia*

The authors and subjects of this series of popular lectures are as follows: Heredity, the general problem and historical setting, by W. E. Castle; the heredity of sex, by C. E. McClung; the inheritance of acquired characters, by J. A. Detlefsen; heredity in relation to cancer, by Maud Slye; the influence of heredity on the occurrence of cancer, by H. G. Wells; eugenics, by M. F. Guyer. The volume contains nothing that is particularly new, but it may be found useful as collateral reading in elementary courses in general biology and genetics.

DIE CHROMOSOMENZAHLEN DER HAUPTSÄCHLICHSTEN GETREIDEARTEN NEBST ALLGEMEINEN BETRACHTUNGEN ÜBER CHROMOSOMEN, CHROMOSOMENZAHL UND CHROMOSOMENGRÖSSE IM PFLANZENREICH. (*Bibliotheca Genetica, Band VIII.*)
By Karl Viktor Stolze *Gebrüder Borntraeger*
9,60 Marks 7¼ x 10⅛; iii + 71 *Leipzig*

In a systematic way this treatise reviews the existing literature on chromosomes in the grains, and presents the author's own results in this field. There follows a brief presentation of data regarding chromosomes in the plant kingdom in general. There is a bibliography of 151 titles. This work will be especially useful to the geneticist for ready reference to this particular aspect of plant cytology.

DIE GENETIK DER KARTOFFEL. (*Bibliographia Genetica I. 1925.*)
By C. Fruwirth *Martinus Nijhoff*
2.50 Florins 6½ x 9¾; 48 *The Hague*

The distinguished plant geneticist, Fruwirth, summarizes critically here the present state of knowledge regarding the genetics of the potato, with an appended bibliography of more than 180 titles. The titles covered are: blossoms and fruit; inbreeding; hybridization; spontaneous variation; grafting; degeneration; and the effect of selection.

GENETIC MONOGRAPH ON PISUM. (*Bibliographia Genetica II. 1925*).
By S. J. Wellensiek. *Martinus Nijhoff*
$2.60 6½ x 10; 134 *The Hague*

This volume reviews critically the extensive literature on the classic form of post-Mendelian genetics, the pea. Teachers of biology will find it a useful reference work in spite of the sometimes quaint English. The bibliography includes something over 180 titles.

HEREDITY IN RABBITS AND GUINEA-PIGS. (*Bibliographia Genetica I. 1925.*)
By W. E. Castle. *Martinus Nijhoff*
$1.00 6½ x 9¾; 40 *The Hague*

Professor Castle divides his authoritative review of the present state of knowledge regarding the genetics of rabbits and guinea-pigs into the following sections:

Introduction; origin of the domestic rodents; coat characters of the rabbit; blending inheritance in the rabbit; the inherited characters of guinea-pigs; historical. There is a bibliography of 84 titles.

GENETISCHE UNTERSUCHUNGEN AN MOOSEN. (*Musci und Hepaticae.*) (*Bibliographia Genetica I. 1925.*)
By F. von Wettstein. *Martinus Nijhoff*
2 Florins 6¼ x 9¾; 38 *The Hague*

This general review of the genetics of mosses (*Musci* and *Hepaticae*) discusses the material under the following headings: Embryology; genetic investigations; crossing experiments; sexuality in mosses. There is a bibliography covering six pages.

GENETISCH-PHYSIOLOGISCHE ANALYSE DER HETEROSTYLE. (*Bibliographia Genetica II. 1925.*)
By G. von Ubisch. *Martinus Nijhoff*
2.80 Florins 6¼ x 10; 56 *The Hague*

This is an excellent review of the present state of knowledge of the genetics of heterostylism in plants. The significance of physiological and environmental factors, as well as purely genetic, in the production of this condition are discussed. There is a bibliography of 81 titles.

UNTERSUCHUNGEN ÜBER DIE FAKTORIELLE KONSTITUTION EINIGER KOMPLEXHETEROZYGOTISCHER ÖNOTHEREN. (*Bibliotheca Genetica, Band IX.*)
By O. Renner *Gebrüder Borntraeger*
22 Marks 7¼ x 10¼; iii + 168 *Leipzig*

This valuable summary of an important series of genetic studies is discussed in detail in this number of THE QUARTERLY REVIEW OF BIOLOGY by Dr. A. H. Sturtevant (*cf. supra*, pp. 283–288).

DIE GATTUNG EPILOBIUM. (*Bibliographia Genetica I. 1925.*)
By Ernst Lehmann *Martinus Nijhoff*
2.80 Florins 6¼ x 9¾; 56 *The Hague*

The author deplores the fact that plants of the genus *Epilobium* have not been as much used for genetic studies as the nearly related genus *Oenothera*. That a beginning has been made in this direction, however, is indicated by the fact that his bibliography of the pertinent literature includes over 177 titles. The review includes a discussion of the general systematic and morphological bases for the use of *Epilobium* as genetic material, followed by sections on the natural hybrids in the genus, and the experimental genetic studies which have so far been carried out.

GENERAL BIOLOGY

BIOLOGIE DER TIERE DEUTSCHLANDS. (*Lieferungen 1–6.*)
Edited by Paul Schulze *Gebrüder Borntraeger*

Lief. 1, 0,81 Marks	43 pp.	*Leipzig*
Lief. 2, 0,9 Marks	55 pp.	
Lief. 3, 1,44 Marks	5½ x 8⅜; 69 pp.	
Lief. 4, 1,8 Marks	77 pp.	
Lief. 5.	52 pp.	
Lief. 6.	64 pp.	

These little treatises represent the beginning of a useful enterprise. The *Biologie der Tiere Deutschlands* will attempt to fill the need for a work which will, within moderate compass, set forth in an authoritative way the important facts regarding the general biology of all the animal groups represented in Central Europe. Separate parts will be contrib-

uted by specialists. Judging by the first six parts, the result, if the project is carried through to completion, will be a first-rate general natural history. The groups dealt with in the parts before us, and the authors, are as follows: *Fresh Water Sponges* by Paul Schulze; *Fresh Water Hydroids* by Paul Schulze; *Classification of the Families of Mites Found in Germany* by H. Vitzthum; *Ixodina* by Paul Schulze; *Thysanoptera* by H. Priesner; *Leaf Mining Insect Larvae* by Martin Hering; *Hydracarina* by Karl Viets; *Eriophyina* by Paul Schulze; *Other Acarina* by H. Vitzthum; *Aranëina* by U. Gerhardt; *Fish* by A. Remane; *Gastrotricha* by Paul Schulze; *Diptera* by E. Lindner; *Turbellaria* by E. Reisinger. The numbers before us are well illustrated and contain brief but useful bibliographies in each case. According to the dates on the parts before us no number seems to have been issued since 1923. It is to be hoped that so promising an enterprise has not come to grief thus early in its career.

SYLLABUS DER INSEKTENBIOLOGIE. (*Lieferung 1.*)
Edited by Hans Blunck. Gebrüder Borntraeger
6 Marks 5½ x 8¾; 136 *Leipzig*

This is the first number of an extremely ambitious undertaking which, if carried through to completion, will be of enormous usefulness not only to entomologists but to biologists in general. What it aims to do is to give a detailed subject index of the data of general biological interest, as contrasted with purely taxonomic interest, in the literature of entomology. An elaborate system of abbreviations and condensations is employed to keep the work within reasonable bounds. We shall watch with the greatest interest the progress of this work. The present number makes a fair beginning on the *Coleoptera*. The general editorship of Dr. Hans Blunck insures that the work will be done with thoroughness.

THE GROWTH OF BIOLOGY.
By William A. Locy. Henry Holt and Co.
$4.00 5¾ x 8¾; xiv + 481 *New York*

This posthumous book by Professor Locy is a valuable addition to the existing manuals on the history of biology. It deals with the history of zoology from Aristotle to Cuvier; of botany from Theophrastus to Hofmeister; and of physiology from Harvey to Claude Bernard. It is in the main written around the lives of the individuals who made the advances in biological science. The book is well indexed and illustrated with 140 text figures. It is distinctly a better piece of work than the author's earlier book, "Biology and Its Makers."

THE BIOLOGY OF POPULATION GROWTH.
By Raymond Pearl. Alfred A. Knopf
$3.50 5¾ x 8¼; xiv + 260 *New York*

The results of the author's most recent studies, experimental and statistical, of various aspects of the population problem are recorded in this book. Most of the material has not been published hitherto. There is a bibliography of 165 titles. The topics discussed, after a general introductory chapter having the purpose of orienting the reader in relation to earlier work, are: The growth of experimental populations of *Drosophila;* the indigenous native population of Algeria; the mortality of the native population of Algeria; the birth rate of the native population of Algeria; the influence of density of population on fertility; the differential birth rate and the

population problem; human behavior and the birth rate.

PROCEEDINGS OF THE ANNUAL CONGRESS ON MEDICAL EDUCATION, MEDICAL LICENSURE, PUBLIC HEALTH AND HOSPITALS. *Held in Chicago, March 9, 10, 11 and 12, 1925.*

Press of American Medical Association

50 cents 8½ x 11½; 134 *Chicago*

A reprint, in convenient form, of the papers and addresses given at the Congress specified in the title. Teachers of pre-medical biology courses will find it useful in getting the point of view of the medical educator.

OUTLINES OF GENERAL BIOLOGY. *An Introductory Laboratory Manual.* *By Charles W. Hargitt and George T. Hargitt.*

Lea and Febiger

$2.00 5½ x 8; vi + 192 *Philadelphia*

The fifth edition of a well-known laboratory guide for an elementary course in general biology. The chief alteration in this edition is the addition of directions for the study of the flatworms, both free living and parasitic.

DIE ISOPOTENZ ALLGEMEIN HOMOLOGER KÖRPERTEILE DES METAZOENORGANISMUS. (*Abhandlungen zur theoretischen Biologie Heft 22.*) *By N. G. Lebedinsky.* *Gebrüder Borntraeger*

3,30 Marks 6½ x 10; iii + 36 *Leipzig*

This small volume deals critically with the somewhat specialized problem of the functional and structural consequences of metamerism. The principal conclusion reached is the one suggested by the title, that generally homologous parts of the body are developmentally isopotent.

HUMAN BIOLOGY

OLD AMERICANS. *By Aleš Hrdlička.*

The Williams & Wilkins Co.

$10.00 6½ x 9¾; xiii + 438 *Baltimore*

This book is a detailed account of an investigation which has been carried on by Doctor Hrdlička for the past fourteen years. It presents extensive data to show just what physically, and in some measure also physiologically, the old American stock represents, and what developmental changes, if any, have already been realized in it, and towards what it is tending. By "Old Americans" are meant in general those American whites who have been longest in this country. In fact the term is restricted in the investigation to mean those Americans whose ancestors on each side of the family were born in the United States for at least two generations. The following are the main topics dealt with: an historical sketch of the Old American stock; pigmentation; measurements and morphological observations, which includes a thorough general anthropometric survey of the individual; physiological observations; discussion of certain general problems on the basis of the data; and finally the future American type. In view of the author's position in the anthropological world it is really unnecessary to state that the work has been done with extreme care and thoroughness, and will stand as a permanent anthropological reference work. The book closes with a detailed index, covering 26 pages.

THE HOMICIDE PROBLEM. *By Frederick L. Hoffman.*

The Prudential Press

6 x 8¼; 106 *Newark, N. J.*

The indefatigable Nestor of American vital statisticians performs once more a

useful service to the student of human biology by bringing together a long series of papers dealing with the statistics of murder, originally contributed to insurance journals which practically never come to the attention of biologists. For the United States he gives detailed records of homicides from 1882 to 1924. In the period from 1900 to 1924 inclusive a vast number of laws intended to make and keep us good have been put upon the statute books of the various commonwealths which compose these United States, as well as upon the records of the doings of the Federal Congress. It is an interesting and grimly humorous fact that the homicide rate per 100,000 of population in 28 of the larger American cities, *doubled* in this period. We are under the impression that students of human biology can obtain this valuable little treatise of Doctor Hoffman's without cost, by application to the Prudential Life Insurance Company of America.

HEALTH CONDITIONS AND DISEASE INCIDENCE AMONG THE ESKIMOS OF LABRADOR.

By Samuel King Hutton. *The Wessex Press*

6 Shillings $7\frac{3}{4}$ x $10\frac{1}{2}$; 74 *Poole, England*

The author of this much too brief book was for seven years a practicing physician among the pure-blooded Eskimos of Northern Labrador. It is an extremely interesting account of his observations on disease among these people. It constitutes a valuable source for the student of human biology in general, and in particular for the philosophically minded student of the problems of public health. These Eskimos live in a harsh environment, where the struggle for physical existence is an ever-present reality. Natural selection eliminates from 40 to 60 per cent of the population before the age of 5 is reached, and the survivors are highly adapted to living under the conditions imposed by their particular environment. Space is lacking here to quote many of the detailed results; only three may be mentioned briefly. The author never saw or heard of a case of malignant new growth in an Eskimo. Among the real meat-eating Eskimos he never saw or found any record suggestive of the occurrence of appendicitis. Regarding tuberculosis, he makes the following interesting observation: It is an introduced disease; there is no evidence that it existed as a natural disease among primitive Eskimo tribes. "It is not a widespread cause of death among the Eskimos, but runs very markedly in certain families."

MEDICAL HEREDITY. *Distinguished Children of Physicians (United States, to 1910.)*

By William Browning.

The Norman, Remington Co.

$4.00 $6\frac{1}{4}$ x $9\frac{1}{4}$; 262 *Baltimore*

This entertaining volume performs a real service to the student of human biology. It provides him with a classified list of American persons who attained some degree of distinction in some field of human activity, and were the children of physicians, the list ending with the year 1910. The fields in which distinction were attained are divided into sixteen general classes, and within each class the names are arranged chronologically by birth date. This list is followed by some 40 odd pages of review and commentary; four appendices; and a general index of names. The book provides a mine of material for the biometrician, not at all exhausted by the rather simple statistical

summaries which are as far as the author himself ventures in this direction. Dr. C. B. Davenport contributes an introduction.

ALLGEMEINE RASSENKUNDE. *Als Einführung in das Studium der Menschenrassen.*

Dr. Walter Scheidt. *J. F. Lehmann*

33 Marks 7 x 10¼; xiii + 585 *München*

This stately and beautifully printed volume is the first in a proposed large work on *Rassenkunde* undertaken by Dr. Walter S. Scheidt in cooperation with Doctors Gero von Merhart, Richard Thurnwald and Ernst Wahle. This introductory volume will be followed by a series on the anthropology of special races, of which the next announced for publication will deal with the races of Europe and the extra-European Mediterranean races. The six sections of the present volume discuss the following subjects: The idea of race in anthropology and the classification of human races (historical review); inheritance in man; the manifoldness of human characters; selection in man; concept of race in human beings; human inheritance, and racial characters. The book closes with extensive indices. It is a significant addition to anthropological literature, which must be in every adequate library of the subject.

THE NEW AGE OF FAITH.

By John Langdon-Davies.

The Viking Press

$2.50 5½ x 8¼; 255 *New York*

This book is a counterblast to the writings of A. E. Wiggam, Lothrop Stoddard, Madison Grant and their ilk. The author is stated to be a journalist and popular lecturer. The problem with which the book deals is the significance of the science of biology, in its modern aspects, for the development and control of human social relations. A rather extreme environmentalist position is emphasized throughout.

THE NATURAL INCREASE OF MANKIND.

By J. Shirley Sweeney, with an introduction by William H. Welch.

The Williams & Wilkins Co.

$4.00 6 x 8¾; 185 *Baltimore*

This book gives an account of a detailed biometric study of the vital index (Birth/Death ratio) of all the populations of the world for which the necessary statistical data are available. An entertaining and historically valuable introduction is contributed by Doctor Welch. There is a bibliography of 86 titles and appendices of the raw statistical data used in the inquiry, which will be useful to other students of the population problem. The book is well indexed, and makes a definite contribution to the much discussed population problem.

CANCER MORTALITY AMONG INSURED WAGE EARNERS AND THEIR FAMILIES. *The Experience of the Metropolitan Life Insurance Company Industrial Department 1911 to 1922.*

By Louis I. Dublin, Edwin W. Kopf, George H. Van Buren.

Metropolitan Life Insurance Co.

6¼ x 9½; 104 *New York*

A detailed analysis of the experience of the Metropolitan Life Insurance Company relative to mortality from cancer. In certain respects the material considerably surpasses in value that which can be derived from official vital statistics. The general conclusions as to the trend of cancer mortality are somewhat

more optimistic than many recent ones have been, which were based upon less adequate material and less careful statistical analysis. The authors are to be congratulated for having produced such an excellent piece of timely bio-statistical research.

ZOOLOGY

THE BIOLOGY OF FISHES.
By Harry M. Kyle. *The Macmillan Co.*
$4.50 5¾ x 8¾; xvi + 396 *New York*

This is a well written and illustrated account, from the point of view of modern biology, of the natural history of fishes. The general topics discussed are: The general characters of fishes; habits in general; migration; development; regulation of the form and structures; economy of the body (1) production and transport of energy, (2) utilisation and emission of energy; variation and differentiation; the genealogy of fishes; distribution of fishes in time and space; adaptations to suit particular conditions; fishes and the web of life; the food question; mental life. A bibliography of some fourteen pages documents the statements in the text. The book closes with a good index.

MANUAL OF INJURIOUS INSECTS.
By Glenn W. Herrick. *Henry Holt and Co.*
$4.50 5¾ x 8¾; xxi + 489 *New York*

This is a thorough, systematic treatise on economic entomology, intended primarily for students of agriculture. The first four chapters are of a general introductory character, and are followed by seven chapters on various methods of control of insects injurious to crops, or in other ways. The remaining chapters of the book deal with the insects injurious to particular crops, taken one by one or in small homogeneous groups. This plan of arrangement involves a good deal of repetition, but is probably the most useful one for the agricultural student. The general zoölogist will find this a handy reference work.

ZOOLOGIE IM GRUNDRISS. (*Lieferungen 1 und 2.*)
By Walter Stempell. *Gebrüder Borntraeger*
Lieferung 1, 6,60 Marks *Berlin*
7⅛ x 10½; xviii + 336
Lieferung 2, 6,90 Marks

These two parts constitute the beginning of a textbook of general zoölogy conceived on broad and inclusive lines. A brief introduction of sixteen pages deals with the underlying ideas and scope of zoölogy; with its different divisions; and finally with its history. Then begins the first main section of the whole work, which discusses the morphology and taxonomy of animals. About 50 pages are given to promorphology, which is taken to mean, in the first instance, the general principles of cytology and histology and, secondly, the ground plan of animal morphology. The remainder of these two parts is taken up with a systematic discussion of the comparative morphology of the different animal groups up to and including the vertebrates. So far as may be judged from these first parts, the work when completed will form a useful and welcome addition to the general textbook literature of zoölogy.

BRITISH BIRDS. Vol. II.
By Archibald Thorburn.
Longmans, Green and Co.
$5.50 6 x 8¾; ix + 130 *New York*

The second volume of this beautifully illustrated handbook of British Birds, of which the first volume was noticed in

No. 1 of THE QUARTERLY REVIEW OF BIOLOGY, deals with six orders, as follows: *Passeres, Picariae, Striges, Accipitres, Steganopodes,* and *Herodiones.* The 48 colored plates in this volume seem even more charming than those in the first volume. While the text is meager in amount it contains many interesting and useful bits of information on habits and life histories.

DIE AMEISENMIMIKRY. *Ein exakter Beitrag zum Mimikryproblem und zur Theorie der Anpassung. (Abhandlungen zur theoretischen Biologie, Heft 19.)*

By Erich Wasmann, S. J.

Gebrüder Borntraeger

9 Marks 6½ x 10; xii + 164 *Leipzig*

This detailed and highly technical review of the facts regarding the mimicry of ants by their guests, ends on a note of high piety. The wisdom and goodness of God seem to be the chief causal factors concerned with the production of adaptive mimicry, with the principle of natural selection as a very second-rate helper. The less spiritual portions of the book will be found useful for reference.

LABORATORY DIRECTIONS IN GENERAL ZOÖLOGY.

By Winterton D. Curtis and Mary J. Guthrie.

John Wiley and Sons

$1.50 5¾ x 9; xxxiii + 194 *New York*

This is a revised and extended edition of similar manuals published at various times since 1912 by the senior author. It represents the accumulated experience of some twenty years development of the beginning course of zoölogy at the University of Missouri. It outlines a splendidly organized elementary course.

A LABORATORY GUIDE IN GENERAL ZOÖLOGY.

By A. Richards. *Lea and Febiger*

$1.75 5½ x 8; viii + 149 *Philadelphia*

The fourth edition, thoroughly revised, of a laboratory guide for a course in elementary general zoölogy. It offers no particularly original features, but the material is well worked out pedagogically.

BOTANY

METHODS OF DESCRIPTIVE SYSTEMATIC BOTANY.

By A. S. Hitchcock. *John Wiley and Sons*

$2.50 6 x 9½; vii + 216 *New York*

In a thorough-going, practical way this book discusses the methodology of systematic botany. The beginner in any sort of taxonomic work has hitherto had to learn the technique of his trade by main strength and awkwardness, or by serving as an apprentice to some expert. With great skill and good judgment Doctor Hitchcock has produced a logical, well-ordered description of both the general principles and the details of this technique. There is no parallel treatise to this on the zoölogical side. Perhaps Doctor Hitchcock's successful achievement will stimulate some zoölogist to write one. In the meantime the beginning taxonomist in the animal world will find much that is helpful to him in this book.

THE AMERICAN OAKS. *(National Academy of Sciences Memoirs, Volume XX.)*

By William Trelease.

Government Printing Office

$3.25 *Washington, D. C.*

9½ x 11¾; v + 255; 420 plates

This is a thorough, detailed and comprehensive revision of the species of the genus *Quercus* found on the North Ameri-

can Continent. It is extensively and beautifully illustrated, and will stand for all time as a monumental piece of research in systematic botany.

A LABORATORY GUIDE FOR A COURSE IN GENERAL BOTANY.
By Lee Bonar, Richard M. Holman and Lucile Roush. John Wiley and Sons
$1.25 6 x 9¼; xvi + 106 *New York*

This is an excellent laboratory outline for a college or university course in general botany, worked out at the University of California, and tested over a five-year period in mimeograph form before being reduced to print. The first part of the course gives the structure and functions of seed-bearing plants, carrying along physiological and morphological work side by side. The second part presents typical examples of the principle groups of plants for study, the work being made to bear directly upon the general principles of classification in the plant kingdom. Why is it that the pedagogy of elementary botany is so much better than that of elementary zoology, generally speaking?

BERGEY'S MANUAL OF DETERMINATIVE BACTERIOLOGY. *A Key for the Identification of Organisms of the Class Schizomycetes.*
By David H. Bergey.
The Williams & Wilkins Co.
$5.50 6¼ x 9¼; xvi + 462 *Baltimore*

This second edition of Bergey's well-known manual of condensed keys and species descriptions, for the determination of the taxonomic position of bacteria, differs from the first chiefly in alterations necessitated by changes in the nomenclatural status of genera, and in the addition of new genera and species described since the book was first issued. It is a standard work in the field. There is an index of genera and species covering twenty odd pages.

GRUNDLINIEN ZUR ENTWICKLUNGSMECHANIK DER PFLANZENGEWEBE. (*Abhandlungen zur theoretischen Biologie Heft 20.*)
By H. Pfeiffer. Gebrüder Borntraeger
6 Marks 6½ x 10; vi + 99 *Leipzig*

This volume presents a critical review of the literature on experimental morphology in the plant kingdom. While it is fair to say that, with a few exceptions, the botanical workers in this field seem to have drawn upon the school of Roux for their guiding ideas, the volume can be read with profit by the experimental animal morphologist.

MORPHOLOGY

A LABORATORY MANUAL OF THE ANATOMY OF THE RAT.
By Harrison R. Hunt. The Macmillan Co.
$1.25 5 x 7¾; vii + 123 *New York*

The author suggests that the rat may well replace the cat or dog as a subject for dissection in college courses in vertebrate anatomy, and offers this manual as a laboratory guide for such use. By deliberate intent the book is not illustrated, which is probably a mistake from the standpoint of its specific pedagogical purpose, and certainly greatly reduces its value as a reference work. The whole treatment is rather elementary and superficial. What is needed is a treatise on the anatomy of the rat comparable in thoroughness and detail to Reighard and Jennings' *Anatomy of the Cat.*

DIRECTIONS FOR THE DISSECTION OF THE CAT.
By Robert Payne Bigelow.
The Macmillan Co.
$0.90 5 x 7¾; xi + 47 *New York*

This is a laboratory guide for the dissection of the cat, arranged to accompany Reighard and Jennings' long and favorably known treatise on the *Anatomy of the Cat*, to which specific page references are given throughout.

LABORATORY MANUAL OF THE FOETAL PIG.
By W. J. Baumgartner. The Macmillan Co.
$0.90 5 x 7¾; xii + 57 *New York*

Owing to the difficulty which the author alleges to exist in obtaining small mammals for material in courses in the comparative anatomy of the vertebrates, or for the mammalian portion of an elementary zoölogy course, the foetal pig is offered as a substitute, and the present volume as a laboratory guide for its dissection. Five general arguments are offered as to why the foetal pig is a good substitute. Three of these arguments seem very feeble indeed, and the fifth rather completely refutes whatever validity might have been supposed to inhere in the other four.

PHYSIOLOGY

ORALE REIZTHERAPIE. *Ein Beitrag zu der Stellungnahme Geheimrat Biers zur Homöopathie.*
By Arnold Zimmer. F. C. W. Vogel
5 Marks 6½ x 9½; 107 *Leipzig*

This book gives a detailed account of an extensive, experimental investigation carried out in the Surgical Clinic of the University of Berlin, undertaken for the purpose of scientifically testing the underlying tenets of homeopathy. The work seems to have been carefully done. The results are somewhat surprising in indicating that perhaps there is more in the homeopathic theory than has commonly been supposed, particularly so far as concerns the size of dosage. The work has general biological interest to the student of *Reizphysiologie*.

REPRODUCTION IN THE RABBIT.
By John Hammond (with foreword and chapter on the formation of the corpus luteum by F. H. A. Marshall.) Oliver and Boyd
15 s. net 6 x 9; xxv + 210 *London*

This book constitutes No. IV of the useful series of Biological Monographs and Manuals of which the General Editors are Dr. F. A. E. Crew and Dr. D. Ward Cutler. It contains the account of a long experimental investigation, with an adequate review of the pertinent literature, on the physiology of reproduction in the rabbit. After a short introductory chapter on material and methods, the book deals successively with reproduction in the male; the female reproductive phases; the formation of the corpus luteum (contributed by Prof. F. H. A. Marshall, F. R. S.); ovulation and the Graafian follicle; the preliminaries to fertilisation; sterility; the effects of lactation; the duration of pregnancy; and a summary of the results. Brief but adequate bibliographies follow each chapter, and there are excellent author and subject indices. This is a book which every laboratory doing biological work of any sort with the rabbit as material, will need on its shelves.

MUSCULAR ACTIVITY.
By Archibald Vivian Hill.
The Williams & Wilkins Co.
$2.75 5⅛ x 8¼; 115 *Baltimore*

This volume contains the sixteenth course of lectures on the Herter Founda-

tion at the Johns Hopkins School of Medicine, delivered in 1924 by the Professor of Physiology in University College, London. They give a condensed account of Professor Hill's own important researches on the physiology of muscle in their relation to the general body of knowledge on that subject. Short bibliographies follow each chapter. The book is well indexed.

INFLUENCE OF THE THYROID GLAND ON OXIDATION IN THE ANIMAL ORGANISM.
By Edward C. Kendall
Columbia University Press
$0.60 6¼ x 9¼; 36 (paper covers) *New York*

This is the lecture given on the occasion of the award to the author of the Charles F. Chandler Medal in Chemistry by the Trustees of Columbia University. It deals with the chemistry and physiological properties of thyroxin, the active principle of the thyroid gland obtained in crystalline form by Doctor Kendall.

LIGHT AND HEALTH. *A Discussion of Light and Other Radiations in Relation to Life and to Health.*
By M. Luckiesh and A. J. Pacini.
The Williams & Wilkins Co.
$5.00 6¼ x 9¼; viii + 302 *Baltimore*

Using "light" in an extended sense to mean "radiant energy" or "radiation," the authors have attempted to give a non-technical account of the present state of knowledge of the effect of light upon living organisms, and particularly man. After three general introductory chapters special chapters are devoted to the influence of light on the blood, the skin, the glands, the skeleton, the muscles, the nerves, the viscera, infectious diseases, hygiene in general, the senses, mental conditions, and health and happiness in general. On some points the book is not at all critical of the evidence, but the most important defect is that throughout there is no indication of the sources from which the evidence is derived. Author's names are mentioned, but there is no slightest indication of where their writings are to be found, or what particular ones are referred to. This omission seriously reduces the value of the book for scientific purposes.

BIOCHEMISTRY

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 178.* Containing following articles: *Verhütung von Laboratoriumsunfällen*, by Ferdinand Flury; *Indikatoren*, by E. E. Chapski; *Charakteristische Kohlenstoff-Stickstoff-Kondensationen der Carbonylkörper*, by Ernst Komm; *Acylieren*, by Fritz Wrede; *Die Veresterung der Carboxylgruppe*, by Franz Bachér. *Urban & Schwarzenberg*
16,20 M. 7 x 10; 384 + xxiv *Germany*

Of the articles contained in this number of the Abderhalden Handbook of Biological Technique perhaps the first two are of the greatest interest to general biology. The first deals with the prevention of laboratory accidents, and the second with the chemical constitution, properties and uses of indicators. Both topics are discussed with genuine Teutonic thoroughness.

MIKROANALYSE NACH DER MIKRO-DENNSTEDT-METHODE.
By Casimir Funk. *J. F. Bergmann*
1,50 Marks 6 x 8¾; 15 *München*

This little pamphlet deals with refinements of microchemical analysis. It is not entirely clear why it was thought necessary to publish these 15 pages as a book rather than as a contribution to some established chemical journal.

OXYDATION UND REDUKTION.
(Handbuch der Biologischen Arbeitsmethoden, Lieferung 174.)
By Richard Stoermer.
Urban & Schwarzenberg
21 Marks 7 x 10; 456 *Berlin*

This part of the Abderhalden Handbook deals in great detail and completeness with the application of different oxydizing and reducing agents to the attainment of particular biological ends. It will be a useful reference work for the biochemist.

SEX

Vacant

(Because of the odd, but true, circumstance that no book falling in this field has reached THE QUARTERLY REVIEW OF BIOLOGY during the past three months.)

BIOMETRY

STATISTICAL METHODS FOR RESEARCH WORKERS.
By R. A. Fisher. *Oliver and Boyd*
15 shillings 6 x 9; ix 239 *London*
+ 6 pp. tables

This volume constitutes No. III of the series of biological Monographs and Manuals under the editorship of Doctors Crew and Cutler. It aims to give the biologist an account of the elementary biometrical technique useful in connection with the treatment of his problems. The viewpoint and methods of treatment are in some respects novel, representing the views of the author, who is one of the most distinguished of mathematical statisticians. While this is desirable and in every respect praiseworthy, it seems a little unfortunate that Mr. Fisher has felt it necessary to use so extensively a new and somewhat confusing terminology. It is probable that on this account the biologist may find this book less useful practically than Yule's *Introduction to the Theory of Statistics.*

VARIATIONS IN THE COMPOSITION OF MILK.
By J. F. Tocher. *H. M. Stationery Office*
£1 1s. 7¾ x 10¾; 195 *Edinburgh*

This is a detailed and thorough biometric study of variation and correlation in the chemical composition of cow's milk. It is a substantial contribution to knowledge, and will stand as a valuable reference work. The author seems entirely unacquainted with the fact that any biometrical work has been done upon this subject in this country.

PSYCHOLOGY AND BEHAVIOR

WHY WE BEHAVE LIKE HUMAN BEINGS.
By George A. Dorsey. *Harper and Brothers*
$3.50 5⅛ x 6¼; xv + 512 *New York*

This non-fiction "best seller," by the one time Associate Professor of Anthropology in the University of Chicago and Curator of Anthropology at the Field Museum, attempts to tell in a volume which can be held in one hand the complete and up-to-date story of the raw materials of human nature and the possibilities of intelligent behavior. This is a large order, and, somewhat as in the case of Samuel Johnson's dog the wonder should be not that the author did not do a better job but that he attempted to do it at all. The whole range of general biology, anatomy, physiology, psychology, and anthropology, not to mention

medicine and hygiene, are called upon to furnish the elements for the account of why we are as we are, and behave as we do. While the turgid and clipped style in which the book is written will be offensive to some, and while others will not agree with the position taken by the author on certain questions, such as behavioristic psychology, it cannot be denied that Doctor Dorsey has produced an entertaining, popular scientific treatise on man. It will be found particularly useful by teachers of general biology for assignment as collateral reading. A brief bibliography and a thorough index complete the volume.

BEHAVIORISM.
By John B. Watson.
The People's Institute Publishing Co.
$3.00 6 x 9; 248 *New York*

An extended review of this book is expected to appear in the next number of THE QUARTERLY REVIEW OF BIOLOGY.

INFLUENCING HUMAN BEHAVIOR.
By H. A. Overstreet.
The People's Institute Publishing Co.
$3.00 6 x 8¼; viii + 296 *New York*

We highly recommend this most entertaining volume to students of human and animal behavior. It concerns the technique of making people, individually or collectively, do what you want them to do. In particular this technique is developed relative to public speaking, advertising, and general writing. The book is well written and authoritative. The appalling thing about it is that it proves so conclusively the precision with which the technique works. Anybody who has any lingering doubts that there may possibly be such a thing as freedom of the will should read this book and see how simple a matter it is for any skillful "go-getter" to make him do precisely what is wanted.

THE THYROID INFLUENCE ON THE BEHAVIOR OF THE WHITE RAT. (*Comparative Psychology Monograph, Vol. II, Serial No. 1.*)
By Edna Rickey.
The Williams & Wilkins Co.
$1.50 6¾ x 9¼; 76 (paper cover) *Baltimore*

A detailed investigation indicated that either an excess or deficiency of thyroid gland substance unfavorably affected the behavior of the white rat. Especially in young animals an excess of thyroid gland substance induced hyperactivity and all learning or improvement in the skill and accuracy in behavior was practically impossible. The results obtained give some suggestion that the effects of alteration from the normal amount of thyroid substance in the body are transmitted to the offspring not themselves subjected to such alterations. Before accepting this conclusion, however, the geneticist will want further critical evidence.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

SINS OF SCIENCE.
By Scudder Klyce. Marshall Jones Co.
$3.00 6 x 9½; 432 *Boston*

We shall allow this book to review itself. We believe that the extensive quotations given will not only entertain our readers, but will also sufficiently fulfil the stated purpose of this department of THE QUARTERLY REVIEW OF BIOLOGY to indicate "the character, the contents and the value of new books."

"So this book is unavoidably novel in several ways:

"(1) It states the answer to the bottom riddle of the universe—states what essential truth or religion really is.

"(2) It shows that the commonsense man practically knows the answer—and always has, since there have been men.

"(3) It shows that the real difficulty about essential truth is that the professional teachers of it, the so-called experts, have been tangled up in words. Hence the book, surprisingly, needs only to show what we common men already know practically:—how words work.

"(4) Because nearly all our leaders have held the riddle of the universe to be impossible of solution, I have become so interested in stating it clearly that I shan't be able (and won't try) to avoid displaying my interest hereafter. And such love of one's job is unfashionable, and hence novel, in this day of scientific detachment, disinterestedness, and cold-blooded neutrality or 'objectiveness.'

"(5) Finally, our intellectuals are teaching basic error, and (refusing to concern themselves with the whole truth) are leading trusting laymen, especially unprotected children, towards destruction. And I am strongly desirous of showing that error clearly, so that we can avoid its perverted teachers and protect our children" (p. 15).

"Indeed, science has never been able to see that the difference in its 'phenomena' is merely a *quantitative* difference of size of reversible components, and not any real difference—all phenomena being *essentially* the same. The reason scientists haven't been able to see that, is simply because they assumed, contrary to sound logic and observed facts and all commonsense, that one or more of the three components could be zero or infinity. In short, they confused One word with Many words.

"I.e., when they couldn't readily see or measure some small quantity, they dogmatically asserted it to be exactly zero—as we have seen repeatedly. Being materialists, they imagined that it was essential that they know such quantitative facts. So they weakly fooled themselves that they did. When they assert that the two transverse forces in gravity are exactly zero, obviously they materialistically assert that One words are Many words—and are wrong" (p. 255).

"You see, these biologists have got a basicly wrong idea of importance and value. They are materialists, or consider *size* or *measures* as being *essential*. They in effect make a foot-rule their God, and worship it—which is idolatry, and plain stupidity.

"In short, it is rigorously proved that God or the universe, judged even by the *definite* requirements of the most materialistic biologists, is living, or a 'person.' The fact that all matter is personal, or alive in the sense of being conscious, is simply a truism of the existence of relationship, and has been seen throughout this book. But detailed proof of it will be given in the chapters on phychology" (*sic*) (p. 312–13).

"Thus it follows that representative leading scientists join with Millikan (as quoted above) in holding that I have not the remotest conception of what I am condemning in this book, have not made the slightest study of the evidence, that I act like a jungle beast, am like a dog, am a menace to democracy and civilization, lend myself as a responsible accomplice to moral and civic crookedness, am blind, prejudiced, unable to overcome a preconception, and intolerant. And I am in effect called all that,even though Millikan has advanced no proof or evidence that I am wrong. Quite to the contrary, he finally wrote me publicly (on March 7,

1924—the preface to his *Sc. and Life* is dated May 3, 1924), stating explicitly that he would agree with me that there can be no such thing as exact science" (pp. 321–22).

"So I should like to call attention to two facts about this book:

"(1) In every case where our common-sense views conflict with orthodox science, I have at least tried to give definite proof, *both* logical *and* evidential, of the correctness of our views. I may be badly mistaken in judging some of the *Many evidence*, and may even logically wabble on a few truisms. But at least I did try to give proof which any normal man could verify directly for himself, without relying on my assertions, or the assertions in any book.

"(2) And in no single instance do I attribute any wrong *motives* to scientists. I.e., I do not accuse any scientists of being somewhat deliberately crooked, or of being intentionally prejudiced, or of having the moral status of a dog or jungle inhabitant. (I sometimes quote their *own words* to that effect—but show that they probably exaggerate their own deficiency.) The sum total of my accusation against intellectuals is that most of them are ignorant, usually to the point of incompetency and often to the point of foolishness or borderline insanity, and that as a result their morals are often extremely bad from *our point of view*, but not intentionally so from *their point of view*. I undertake to *prove in considerable detail* that accusation I bring against them of ignorance. In no case do I accuse them of being voluntarily a menace—although they are dangerous to our welfare if we believe their false doctrines.

"Finally, the 'worst' specific action I recommend against them, is that we stop paying serious attention to them, warn our children against the danger of believing them, and stop paying their salaries and endowments out of *our* pockets, *until* such time as *they* either stop teaching the materialism and agnosticism which we believe is false, or else convincingly *prove* to us that those doctrines are correct. They are of course at *liberty* to teach their dogmatic falsehoods if they wish—*but at their own expense*. They aristocratically or dualistically assume that because they are *superior* to us, therefore they are *privileged* to draw salaries from us to teach what *we* value at less than nothing. Any normal child who is a good American has better sense than to believe such divine-right-of-kings-or-professors (Chap. 17, §2).

"At present we do not believe their doctrines. Further, for nearly fifteen years I courteously and friendlily submitted to them a definite and explicit disproof of those doctrines; and not once did they even *try* to rebut such proof. Invariably, those who don't accept the proof act in one of these three ways: (1) they ignore the proof; (2) they call names, as Millikan has been quoted as doing; or (3) they say 'Hush, Darling.'

That recommended specific action (of letting the scientists finance their errors), obviously is not intolerance on our part *in any Many sense*. It gives them ample opportunity to examine the evidence and correct their errors if they like. But if they do not wish to, or if they can't (usually, they have badly spoiled their minds, and simply can't), the extremest action against them is to protect our children from them, and stop paying them to propagate their error. When Millikan, in the typical scientific way, talks of such mild action as being wicked, he plainly shows that such action is needed.

"I submit Millikan and his colleagues' own statement of their case and my statement of the case, to you, for you to judge. The intellectuals have repeatedly told me

in one way or another that I am unfair and am not sufficiently tolerant and patient. You can judge for yourself" (pp. 322–34).

The chief bibliographic source cited throughout the book is the *Encyclopaedia Brittanica* (*sic*). There is an index.

SCIENCE AND SCIENTISTS IN THE NINETEENTH CENTURY.

By Robert H. Murray. The Macmillan Co. $5.00 6 x 8¾; xvii + 450 *New York*

This falls only a little short, in a few particulars, of being a great book. It is a realistic history of science in the nineteenth century, which proves, with the most elaborate documentation, that within that period substantially every important new discovery and important new idea in the realm of science met with the bitter and determined opposition of scientific men as a group. The leaders of this opposition always included many, if not the majority, of the most distinguished scientific men of the time. The author is a clergyman who is at the same time a trained historian. The motive underlying the writing of the book is to show that scientific men as a class are not a whit more open minded to new ideas than are theologians as a class. To the shame of scientific men it must reluctantly be admitted that Mr. Murray comes uncomfortably near to proving his case. Nor is this unfortunate situation improved by the specious argument of some apologists for science, who have discussed Mr. Murray's book, to the effect that critical skepticism is an integral part of science. It can be too easily shown that science has many times taken to its bosom the most arrant quackery without the slightest critical examination. In fact a strong case could be made that, in the whole intellectual history of mankind, pseudo-science of all sorts has never flourished so extensively and respectably as it has in this twentieth century of grace. The most serious criticism of the book which can be made is that undue emphasis is given in some cases to relatively unimportant people and unimportant discoveries. The chapter headings are as follows: Jenner and Vaccination; Simpson and Chloroform; Lyell and Uniformitarianism; Helmholtz, Joule, and the Conservation of Energy; the Precursors of Darwin; Darwin and Evolution; Pasteur and Microbes; Lister and Antiseptics; Forgotten Scientists; Limitations of Scientists. There is a bibliography covering some 18 pages, and the book is well indexed.

MICROBE HUNTERS.

By Paul de Kruif. Harcourt, Brace and Co. $3.50 6 x 9; 363 *New York*

Objectively this is a history of the development of the science of bacteriology, in the form of biographical sketches of a dozen or so outstanding personalities in that development. But such a cold statement does not do justice to this book. For it is written *con amore*. On every page it is plain that the one passionate intellectual interest of Doctor de Kruif's life has been bacteriology. For him there are no heroes like its makers and no story so thrilling as theirs. A vast amount of painstaking research has obviously gone into the making of this book. The style in which it is written will offend the taste of many persons, as will also its naïve enthusiasms. Furthermore his probably sound estimate of Pasteur will bring down the wrath of those who in effect deify that great man. But in spite of all these considerations it remains the fact that the book is fascinatingly and thrillingly interesting.

Experimental tests show that he who begins at any point to read it is lost for the next two or three hours. And the guess may be hazarded that anyone who starts out to trip up Doctor de Kruif on his factual basis will find that he has essayed a tolerably difficult task.

ÜBER DIE LOGISCHEN PRINZIPIEN DER ÄRZTLICHEN DIAGNOSE. (*Abhandlungen zur theoretischen Biologie Heft 2.*) *By Fritz Mainzer. Gebrüder Borntraeger* 3 Marks $6\frac{1}{2}$ x 10; iii + 51 *Leipzig*

The problem with which this volume has to do offers many entertaining possibilities, but unfortunately the treatment of it here falls a bit on the ponderous, not to say dull, side. The book is an attempt at a philosophical examination of the underlying principles of clinical diagnosis. It examines, in considerable detail, the logical foundations of actual present practice in diagnosis, points out logical weaknesses in the procedure, and suggests logical improvements. There is considerable discussion of the theory of probability in relation to clinical diagnosis. Somewhat unfortunately, there is no attempt at a systematic review of the literature which has dealt with the underlying philosophy of clinical work.